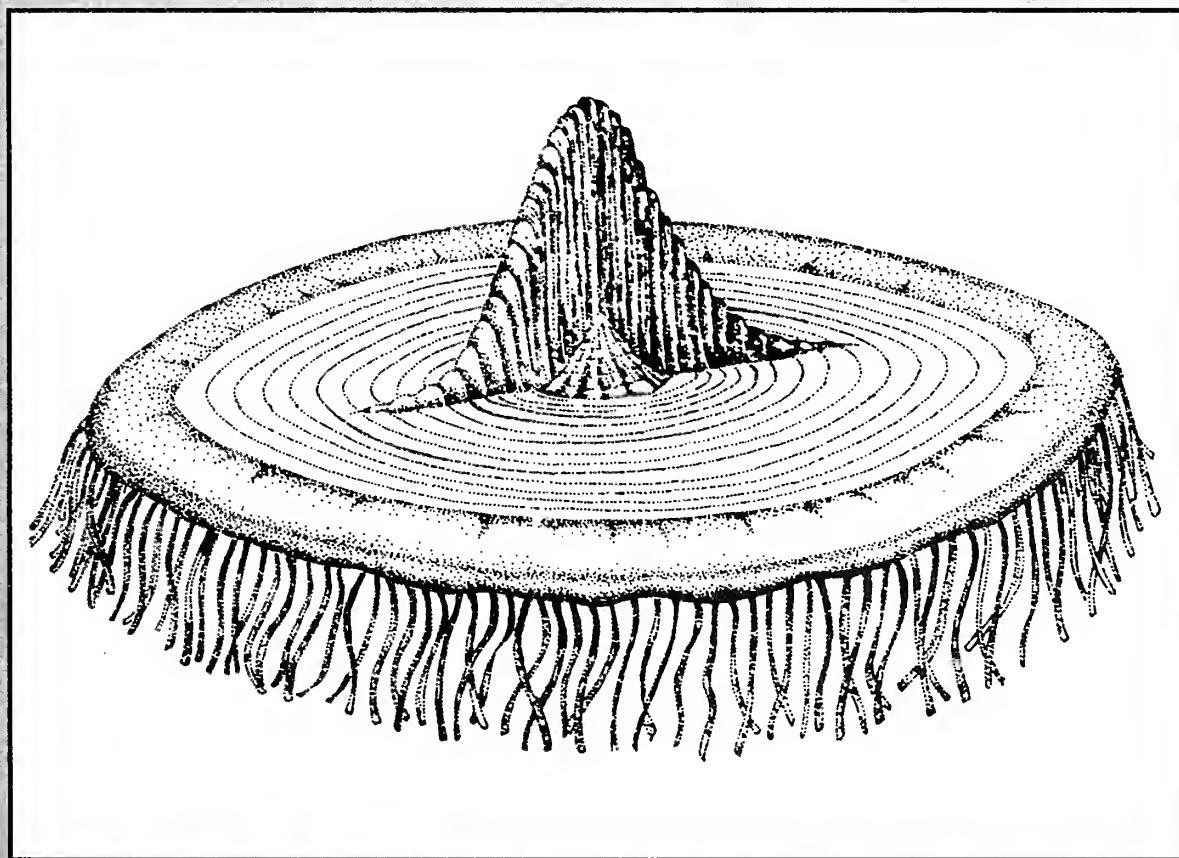


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STUDIES IN STRATIGRAPHY AND PALEONTOLOGY IN HONOR OF DONALD W. FISHER

ED LANDING, EDITOR



BULLETIN NUMBER 481

1994

NEW YORK STATE MUSEUM

The University of the State of New York / The State Education Department

**Cover illustration: *Silurovelella casteri* Fisher, 1957,
a late Silurian chondrophore from New York State**

STUDIES IN STRATIGRAPHY AND PALEONTOLOGY IN HONOR OF DONALD W. FISHER



DONALD W. FISHER

GEOLOGICAL SURVEY

BULLETIN NUMBER 481

1994

N E W Y O R K S T A T E M U S E U M

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Dedication: Donald W. Fisher State Paleontologist 1955-1982

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A personal introduction (EL)

Dr. Donald W. Fisher served as the sixth State Paleontologist of New York State. However, this simple introductory sentence does not convey the importance of Don's role in the science of paleontology, his service to the geological synthesis of New York State and to the exhibits of the New York State Museum, or his role as a mentor to dedicated amateur fossil collectors and young people who eventually became geologists. It is for these reasons that a *Festschrift* in honor of Dr. Fisher has been published. The wide range of reports in this volume mirror the diversity of popular and technical publications he produced during his career.

I am pleased to have had the opportunity to organize, edit, and contribute in a small way to the reports in this Bulletin, because Don Fisher had a significant role in my own development as a paleontologist. My first acquaintance with Don was during a vacation to New York State. This trip featured a visit to the "Petrified Gardens" just northwest of Saratoga Springs, where I bought a number of fossils that were for sale. I was probably eight or nine years old at the time, and brought the fossils to the New York State Museum for identification. My interest was not in what type of fossils they were, but in the precise generic and species names. Don treated this young "walk-in" to the Museum with genial courtesy and, amazingly to me, identified to the species level all of the Black River and Trenton Group fossils I had brought in. As I was leaving, he suggested, "Son, in the future, collect your own." I felt a little humiliated by this comment and considered it a gentle reprimand that I took to heart.

I kept in contact with Don over the years, and during the summers began to collect fossils both in New York and back home in eastern Wisconsin. Don was always helpful, and even identified specimens I sent to him through the mail. If he felt that someone else might be more appropriate in identifying the material, he would return the specimens and include a specialist's address.

My senior honors and master's theses and doctoral dissertation all involved at least some field work in eastern New York, because Don had helped show me the diversity of stratigraphic and paleontologic topics that were available. During these years, Don was always there with helpful suggestions for useful localities that should be investigated.

My own employment with the New York State Geological Survey began in 1981, near the end of Don's service with the State. After all of the years of contact, I had become a colleague of his. In September 1986, I organized the first United States meeting of the Canadian Paleontology and Biostratigraphy Seminar during the Survey's sesquicentennial year. At the banquet, Don read a history of the contributions made by New York's State Paleontologists and introduced me as the seventh State Paleontologist. Many thanks, Don.

Fisher's life and interests (EL, EY)

Donald William Fisher was born in Schenectady, New York, the son of William John and Irene Elizabeth (Tree) Fisher, on September 8, 1922. The family later moved to Buffalo, where he graduated with honors from both Public School No. 24 and East High School. An important feature of his life in Buffalo was the development of a fascination with natural history. The family lived only one city block away from the Buffalo Museum, and Don was enrolled during his elementary school years in several week-long field trips that were organized by the Museum. In addition to offering him the experience of overnight camping in Allegany State Park, the Museum staff provided instruction in field biology and geology. His student days continued at the University of Buffalo, where he received a B.A. (1944) and an M.A. (1948) in geology, and at the University of Rochester (Ph.D., 1952).

Don's early teaching experience included two years as a teaching assistant at the University of Buffalo. Most of his time as a Ph.D. candidate was actually spent back in Schenectady, where he taught geology at Union College. A former student described him as a steady, never-flamboyant lecturer who always imparted large doses of information about fos-

sils and stratigraphy. He was highly regarded as an instructor who was willing to spend extra time with those who were interested in ancient life.

Fisher's association with the New York State Geological Survey began while he was in graduate school. He was hired as Temporary Field Geologist during the summers of 1947 to 1949, and as Provisional Senior Paleontologist in the summers of 1951 and 1952.

His employment with Union College ended in 1953, when he became permanently employed by the Geological Survey. Don Fisher's first title was Senior Paleontologist, and he became State Paleontologist in 1955 after the retirement of Winifred Goldring. A second important development in that year was his marriage to Mary Elizabeth Gibson on July 16, 1955. Don and Betty moved to Kinderhook, New York, where they raised their two sons, Wayne Lee and Dale Scott Fisher.

As State Paleontologist, Don enthusiastically assumed responsibility for collating information on the biotic and stratigraphic sequence for New York State. His own interests centered primarily on the Cambrian and Ordovician, and his colleague, Lawrence V. Rickard, specialized in Silurian and Devonian litho- and biostratigraphy.

All of the geological systems of New York State appear in Fisher's list of popular and technical publications. Among the most important and widely distributed of these were the early correlation charts for the Cambrian, Ordovician, and Silurian Systems of the State (New York State Museum Map and Chart Series 1-3). A revised edition of the Cambrian and Ordovician, which also included Hadrynian strata, appeared in 1976 (NYSM Map and Chart Series 25).

Fisher's career as a paleontologist and stratigrapher was supplanted in the second half of his tenure with the State by his interests in the geological synthesis made available by mapping projects. He was involved with Yngvar Isachsen and Larry Rickard in compiling the five sheets of the 1970 Geologic Map of New York. This interest in geological mapping is also seen in his maps of the Plattsburgh-Rouses Point Quadrangles, the central Mohawk River Valley, and the Glens Falls-Whitehall region (NYSM Map and Chart Series 10, 33, and 35, respectively).

This concern with geological synthesis was highlighted by Don's activity over the years in regional field conferences. He was involved with the organization of five field trips for the New York State Geological Association, three for the New England Intercollegiate Geological Conference, and three for the Society of Economic Paleontologists and Mineralogists.

Don's résumé includes seven reports published before he entered State service and seventy-nine papers during and after his tenure with the Geological Survey. His first relatively long report (twenty-six pages), titled "Lower Ordovician (Canadian) stratigraphy of the Mohawk Valley, New York," appeared in 1954 in the *Bulletin of the Geological Society of America*. This study was based on his doctoral dissertation at the University of Rochester ("Lower Ordovician Stratigraphy and Paleontology of the Mohawk Valley," 1952, 248 p.) and on field work completed with the Geological Survey.

Fisher's publication list would have been even longer had he not given so freely of his time to others. He was on many thesis committees at Rensselaer Polytechnic Institute, and it was a rare year when he did not give at least four or five talks to non-professionals. His pamphlet "Paleontology in a Nutshell" was distributed by the thousands by the Paleontological Society. He also worked with Larry Rickard during the early 1960s to develop about 90 percent of the paleontological exhibits in the old State Museum building.

Don played an important role in the State legislature's selection of *Eurypterus remipes* as the New York State Fossil in 1984. He provided information and support to a group of New Yorkers who preferred this Late Silurian eurypterid over two other candidates, the Middle Ordovician snail *Maclurites* and the Middle Devonian trilobite *Phacops rana*. Fisher believed that a morphologically complex fossil, such as a eurypterid, would interest more people and could help develop a greater interest in geology among non-professionals.

Fisher's retirement in 1982 began a new, personally rewarding phase of his life. He finished the manuscript and maps for the geology of the Glen Falls – Whitehall region shortly after retirement (NYSM Map and Chart Series 35), and taught physical and historical geology for several years at Greene County Community College. However, his activities continue to center around his home in the village of Kinderhook, about a half-hour's drive to the southeast of Albany. Betty Fisher passed away in the Fall of 1993, but Don continues to run the "O.K. Rock Shop" without her help. The name of this shop is an abbreviation of "Old Kinderhook", a nickname for President Martin Van Buren, who was born in, and was a lifelong resident of, the village.

The serious and deliberate approach Don took to his science carries over to the hobbies he enjoys in his retirement. He does not casually collect postage stamps; rather, he is a specialist on the philatelic portraiture of fossils. He also raises roses, which regularly take prizes at regional competitions. More recently, he has added cacti to his greenhouse.

The conoidal fossils (EY)

The fossils that are particularly associated with Don Fisher's paleontological activity are the enigmatic conical remains that are most common in the Lower and Middle Paleozoic. These include hyoliths and a large number of problematical animals known from small, calcareous and phosphatic, tube-like shells. Fisher monographed these for the 1962 edition of Part W of the *Treatise on Invertebrate Paleontology* (pages W98-W143).

My interest in the small conoidal fossils from the Devonian gave me my first field contact with Don Fisher. I flew to Albany in October 1967 and received information from Don about collecting localities near Buffalo. I then picked up the oldest car that I have ever seen from the federal motor pool and drove off to meet Bedřich Bouček, the distinguished Czech paleontologist. We collected near Buffalo and drove east to meet Don in the central part of the State. He took us to several remarkable localities where Professor Bouček gathered sample after sample to compare with the genera and species he had described from the Prague Basin.

The weather got worse, and one of my recollections is stopping in a snow squall at an enormous automobile graveyard so that Professor Bouček could take pictures. The starter on my car was failing, and I was not certain that it would start again after each of our stops. Late in the afternoon on the second day, we stopped for coffee about forty miles west of Albany, and this time the car would not start. After two aggravating hours, it was obvious that the battery had failed. Despite my caterwauling, Don just took the events in stride. He stated matter-of-factly that it was too dark to look at another locality, and we all drove off in his car. Rather than dumping us in a hotel in Albany, he drove to Kinderhook and told Betty that there were two guests for dinner who would also be staying the night.

Acknowledgments (EL)

“Studies in Stratigraphy and Paleontology in Honor of Donald W. Fisher” was made possible by assistance from D. Jorhov (typing and disk preparation), J. Lauber (technical editing), J.C. Finley (galley editing), and G. Nottis (computer assistance). The authors of technical reports are thanked for the timely preparation and revision of manuscripts. Reviewers are indicated in the “Acknowledgments” of each report. EL contributed \$100 toward publication of this Dedication from the Paleontology Fund of the New York State Museum.

Conodont biostratigraphy and biofacies of the Jacques Cartier River Ordovician section, Quebec

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Abstract

Biostratigraphically diagnostic *Amorphognathus superbus* Zone conodonts occur in the *Orthograptus ruedemanni* graptolite Zone in the Utica Shale–Neuville Formation boundary interval along the Jacques Cartier River. Specimens of *A. superbus*, the zonal index of the *Amorphognathus superbus* Zone, have also been found as low as about 75 m below the top of the Neuville Formation in a section along the St. Lawrence River at Neuville. These conodont occurrences show that a portion of the *Amorphognathus superbus* Zone is coeval with a part of the *Orthograptus ruedemanni* Zone. This is in agreement with less-conclusive data from Ohio and New York State that suggest that the base of the *Amorphognathus superbus* Zone corresponds to a level somewhat above the base of the *Orthograptus ruedemanni* Zone. Because the base of the *Amorphognathus superbus* Zone is coeval with a level in the upper part of the *Diplograptus multidentis* Zone in Baltoscandia, it is concluded that the base of the *Orthograptus ruedemanni* Zone corresponds to a level within the European *Diplograptus multidentis* Zone. The conodont fauna of the samples investigated is closely similar to some coeval faunas in the Cincinnati region and in New York State, and represents the *Phragmodus undatus* biofacies that is characteristic of depositional environments well below wave base.

Introduction

The geologic setting and general stratigraphy of the section in the upper Neuville Formation and the basal Utica Shale along the Jacques Cartier River have been summarized by Goldman and Mitchell (this volume). The Jacques Cartier River section is located 2.4 km downstream from Pont Rouge and about 35 km WSW of Quebec City. As noted by Riva (1969, 1972), the section along the Jacques Cartier River (JCR) has particular stratigraphic interest because it exhibits a continuous graptolite succession from the *Orthograptus ruedemanni* Zone to the *Climacograptus (D.) spiniferus* Zone. Such sections are rare because, with the exception of the Mohawk Valley in New York State, a prominent stratigraphic gap exists in this interval in most regions of northeastern North America (Riva, 1972, fig. 16). The JCR section is also important in that its graptolite-bearing shales are interbedded with limestones that contain both graptolites and conodonts and provide an opportunity to integrate conodont and graptolite biostratigraphy. Although many graptolite–conodont zonal ties are now known from the Ordovician (Bergström, 1986), no such direct tie has previously been

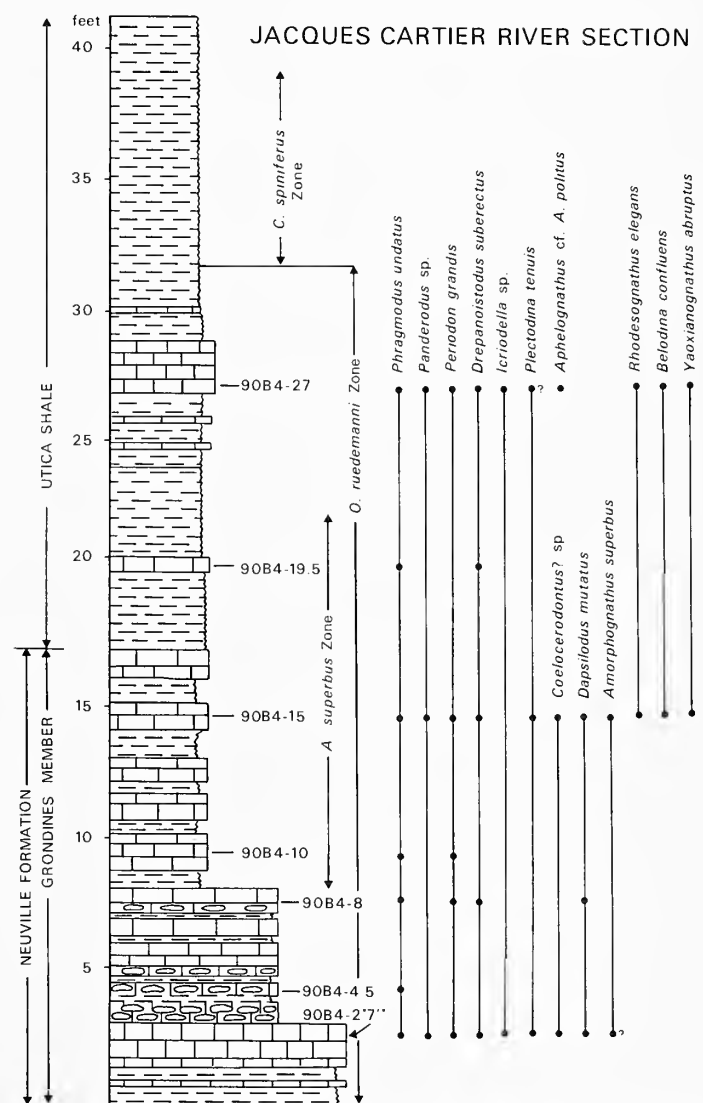


Figure 1. Lithologic succession, levels of conodont samples, ranges of conodont species, and biostratigraphy of the Jacques Cartier River section. Note that the *Orthograptus ruedemanni*–*Climacograptus spiniferus* Zone boundary is stratigraphically above the range of *A. superbus*, the index of the *Amorphognathus superbus* Zone. This shows that the base of the former zone is above the base of the *Amorphognathus superbus* Zone.

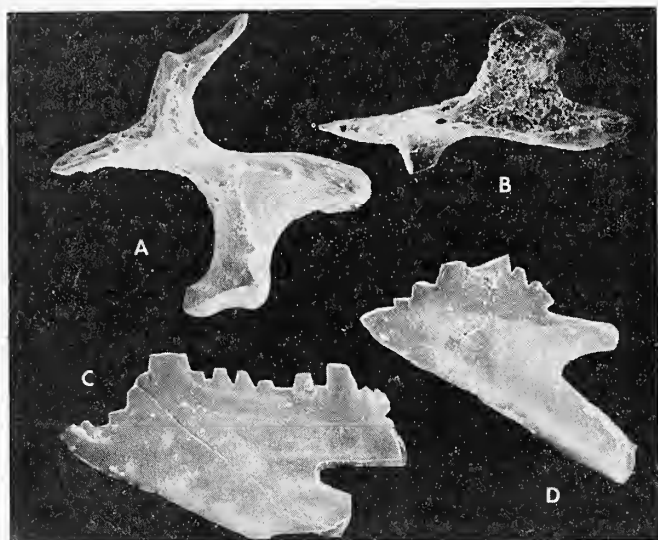


Figure 2. SEM photomicrographs of conodont elements from the uppermost Grondines Member (*Orthograptus ruedemanni* Zone) of the Jacques Cartier River section. All specimens are from sample 90B4-15 and are kept in the type collection of the Orton Geological Museum (OSU), The Ohio State University. A, *Amorphognathus superbus* Rhodes, upper view of dextral Pa element. x85. OSU 46821. B, same species, upper view of sinistral Pa element. x85. OSU 46822. C, *Phragmodus undatus* Branson and Mehl, lateral view of S element with large basal funnel. Note the long anterior process along the lower margin of the funnel. x65. OSU 46823. D, same species, lateral view of another S element with well-developed basal funnel. x65. OSU 46824.

documented within the *Orthograptus ruedemanni* Zone (Bergström, 1986, fig. 4). Finally, the fact that the JCR section exhibits a transition from relatively shallow-water limestone facies to relatively deeper-water siliciclastic facies makes it potentially useful for study of the vertical sequence of depth-related conodont biofacies that were differentiated during a transgressive episode.

A series of rock samples collected by the junior author was processed for a conodont study. The stratigraphic level of each of these samples is shown in Figure 1. Each sample (ca. 2 kg) yielded more than five hundred conodont elements. In addition, several hundred elements of *Phragmodus undatus* Branson and Mehl, the dominant species in all JCR samples, and a smaller number of elements from a few other common species, were not picked from the residues. Although in most cases somewhat broken, the conodont elements are, in general, well-preserved. Many specimens, particularly in sample 90B4-15, have retained very prominent basal funnels (Figure 2C, 2D). Such structures are particularly well-developed in S elements of *Phragmodus undatus*. Indeed, the best preserved specimens show that the basal funnel is much larger and that the anterior process is considerably longer than is apparent in many descriptions published earlier of this common species. Most specimens show a color alteration index (CAI) of 1 to 2, but a few elements, most of which are larger, have a significantly darker color (CAI 3 to 4).

Biostratigraphy

No record of conodonts from the JCR section has previously been published. Globensky and Jauffred (1971) described conodont faunas from a few other exposures of the Neuville Formation in the Neuville area, and their study remains the only comprehensive report on conodonts from the late Middle Ordovician of the St. Lawrence Lowlands.

The collection examined for this report, which comes from the uppermost part of the Grondines Member of the Neuville Formation, includes thirteen multi-element species. About the same number of multi-element species was recorded by Globensky and Jauffred (1971) from the Grondines Member. Among these, two relatively uncommon species, namely *Staufferella falcata* (Stauffer) [= "*Distacodus falcatus*"] and *Protopanderodus liripipus* Kennedy et al. [= "*Scolopodus insculptus*"], are not present in this report's collection. However, specimens of *Belodina confluens* Sweet and *Yaoxianognathus abruptus* (Branson and Mehl) (formerly *Bryantodina? abrupta*, see Bergström, 1990) were recovered in this study. The first species was not found by Globensky and Jauffred (1971), and they listed the latter species only from the lower part of the Neuville Formation (St. Casimir Member). The range of each species and its occurrence in the samples investigated in this report are shown in Figure 1. Because no previously undescribed species were found, and the taxa present are well-known and adequately illustrated in the recent literature and by Globensky and Jauffred (1971), figures of only the zonal index *Amorphognathus superbus* Rhodes and *Phragmodus undatus* (with basal funnels) are provided (Figure 2).

The JCR species association does not differ significantly from that of the lower part of the *Amorphognathus superbus* Zone in the Denley Limestone of New York (Schopf, 1966; Sweet, 1984) and in a coeval interval of the Lexington Limestone in Kentucky and adjacent parts of Ohio (Bergström and Sweet, 1966; Sweet, 1979, 1984). The recovery of typical representatives of *A. superbus* in sample 90B4-15 is of particular biostratigraphical interest because it proves that the middle portion of the JCR section, at least, belongs to the *Amorphognathus superbus* Zone of the Atlantic conodont zonal scheme (Bergström, 1971). The presence of *Belodina confluens* indicates an age no older than the *confluens* Zone of Sweet (1984, 1988), and there is little doubt that the JCR section belongs in that zone of the Midcontinent zonal scheme. The presence of *Periodon grandis* (Ethington), *Rhodesognathus elegans* (Rhodes), *Dapsilodus mutatus* (Branson and Mehl), and *Yaoxianognathus abruptus*, although all relatively long-ranging species, is in agreement with this zonal assignment. Interestingly, the more than one hundred specimens of *Dapsilodus mutatus* recovered in this study are not associated with a single geniculate element. This fact supports Löfgren's (1978) opinion that the apparatus of this species did not include such elements.

Recent studies on the conodont-graptolite zone relations in the Cincinnati region (Mitchell and Bergström, 1991; Bergström and Mitchell, 1990, this volume) suggest that the *Amorphognathus tvaerensis*-*Amorphognathus superbus* zonal boundary corresponds to a level within the *Orthograptus ruedemanni* Zone in the graptolite succession. This conclusion is based mainly on the fact that specimens of *O. ruedemanni* were found both above and below this conodont zone boundary in two drill cores from southwestern Ohio. The investigation summarized herein provides direct evidence that *A. superbus* occurs below the lowest occurrence of *Climacograptus* (*D.*) *spiniferus* in the upper *Orthograptus ruedemanni* Zone.

The data at hand are insufficient to establish the precise level of the base of the *Amorphognathus superbus* Zone within the *Orthograptus ruedemanni* Zone. In all probability, it is well below the base of the JCR section. This is shown by the recovery of typical elements of *A. superbus* in a sample collected about 75 m below the top of the Neuville Formation in the type section of the Grondines Member along the shore of the St. Lawrence River at Neuville. Clearly, additional

study is needed to clarify the range of the lower part of the *Amorphognathus superbus* Zone in terms of the graptolite zonation. An additional biostratigraphic complication in this stratigraphic interval is the fact that *Climacograptus* (*D.*) *spiniferus* appears well below the top of the range of *Orthograptus ruedemanni* and near the *Amorphognathus tvaerensis*–*Amorphognathus superbus* zonal boundary in the Middletown core in southwest Ohio (Bergström and Mitchell, 1990, fig. 4; Mitchell and Bergström, 1991). This fact suggests that the level of appearance of *Climacograptus* (*D.*) *spiniferus*, which in New York–Quebec is taken to mark the base of the *C. (D.) spiniferus* Zone, is diachronous between New York–Quebec and Ohio.

It is significant that the base of the *Amorphognathus superbus* Zone is in the upper part of the *Diplograptus multidens* Zone in Baltoscandia (Bergström, 1971, 1986), and that *Climacograptus* (*D.*) *spiniferus* first appears in the middle to upper part of the overlying *Dicranograptus clingani* Zone (see, for instance, Podhalanska, 1980). This relationship suggests, contrary to some recently published correlations (see, for instance, Bergström, 1986; Finney, 1986), that the base of the North American *Orthograptus ruedemanni* Zone is coeval with a level below, rather than above, the top of the European *Diplograptus multidens* Zone.

Biofacies

As noted above, the JCR section represents a gradual change in the depositional environment from carbonate deposition in relatively shallow water to siliciclastic sedimentation in deeper water. Although the environmental parameters that controlled the distribution of conodonts in time and space are still poorly understood, recent work on Middle and Upper Ordovician faunas of the North American Midcontinent has revealed a striking biofacies differentiation (Sweet, 1988). Lateral biofacies differences are defined by the distribution and relative frequency of important conodont taxa in different environments from shallow to deeper water. As noted above, the JCR fauna is very similar to that present in coeval strata in the Cincinnati region, and it is, therefore, of interest to examine how this fauna fits into Sweet's (1988) biofacies model. About 80% of the elements in the JCR collection belong to *Phragmodus undatus*, and elements of *Plectodina*, *Icriodella*, and *Amorphognathus* total less than 5%. Significantly, no specimens of

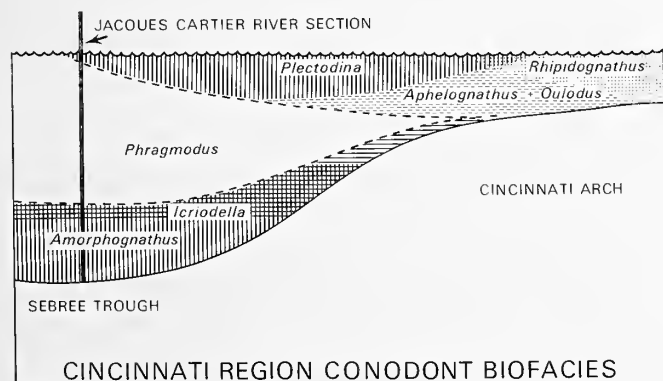


Figure 3. Projected position of best fit between the Jacques Cartier River section and Sweet's (1988, fig. 7.3) Middle–Upper Ordovician conodont biofacies model for the Cincinnati region. Elements of *Amorphognathus*, *Icriodella*, and *Plectodina* are rare in the JCR section, which is strongly dominated by *Phragmodus undatus*.

Oulodus or *Rhipidognathus* have been recovered, and *Aphelognathus* is represented by just two elements from one sample. Among the remaining JCR species, elements of *Dapsilodus mutatus* and *Rhodesognathus elegans* are the most common, but none of these species reaches a frequency of 5% of the total collection.

If the JCR collection is compared with Sweet's (1988, fig. 7.3) model, the best fit is in the position shown in Figure 3, which represents a relatively deeper-water environment characterized by the *Phragmodus undatus* biofacies. Sweet's (1988, p. 156) statement that *Phragmodus undatus* was "...the principal inhabitant of oxygenated well-lit water above the colder bottom-water mass" and "offshore of the more shoal-water, high-energy, or tidal-flat areas..." is in good agreement with lithologic evidence of the depositional environment of the JCR section. The present study, and the distribution data presented by Globensky and Jauffred (1971), suggest that the *Phragmodus undatus* biofacies prevails throughout the Neuville Formation, and that the relative frequency of *Periodon grandis* and *Dapsilodus mutatus* shows an increase toward the upper part of the formation. This is in agreement with the interpretation that the latter two species apparently preferred deeper-water environments in the Middle Ordovician of the North American Midcontinent and, in the case of *Periodon*, "occurred at times of maximum transgression" (Barnes and Fähræus, 1975, p. 139).

Summary remarks

The present study shows that the conodont fauna of the Neuville Formation–Utica Shale boundary interval can be readily referred to the conodont biostratigraphic and biofacies framework established in recent years for the Middle Ordovician of the North American Midcontinent. Biostratigraphically, the JCR section is interpreted as belonging to the lower part of the *Amorphognathus superbus* Zone of the North Atlantic zonal succession and to the *confluens* Zone of the Midcontinent zone succession. In terms of Middle Ordovician Midcontinent biofacies, the JCR section is a typical representative of the *Phragmodus undatus* biofacies, which was previously best known from the Cincinnati region. Perhaps the principal significance of the conodonts in this section is the occurrence of *Amorphognathus superbus* Zone conodonts in association with index graptolites of the *Orthograptus ruedemanni* Zone. This co-occurrence provides a biostratigraphically important tie between the conodont and graptolite zone successions within a stratigraphical interval where such a direct and reliable tie was not known previously.

Acknowledgments

C.E. Mitchell and J.E. Repetski kindly reviewed the manuscript and provided constructive comments. We are also indebted to L.E. Babcock, B. Daye, H. Hayes, S. Leslie, J. Mitchell, and K. Tyler for technical assistance.

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Regional relationships between late Middle and early Late Ordovician standard successions in New York and Quebec and the Cincinnati region in Ohio, Indiana, and Kentucky

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Abstract

The regional relations between the standard Mohawkian Series and the standard Cincinnati Series are assessed using a combination of geophysical, biostratigraphic, and lithostratigraphic evidence. Two cross-sections based on wells, one extending from southwestern Ohio into north-central New York, and another between north-central New York and the Quebec City area, Quebec, illustrate the upper Middle and lower Upper Ordovician facies relations from the Seabee Trough and Lexington Platform in the southwest across the Trenton Shelf to the Taconian Foreland Basin in the northeast. Indications from conodont and graptolite biostratigraphy, K-bentonite bed correlations, and tracing of geophysical log markers suggest that some lithostratigraphic units are recognizable across vast areas. This is interpreted as evidence that surprisingly uniform conditions prevailed in the environment of deposition over much of the craton in eastern North America during late Middle and early Late Ordovician time. However, the lithology and faunas of coeval rocks in the Taconian Foreland Basin differ markedly from those of the cratonic interior, and the former region represents a deeper-water environment that received a large influx of clastic materials from the Taconian highlands in the east. Lithostratigraphic and biostratigraphic data suggest that the base of the type Cincinnati Series corresponds to a level in the basal 5-10 m of the Cobourgian in New York; that the same stratigraphic horizon is in the middle part of the *Climacograptus spiniferus* Zone; and that the base of the *Geniculograptus pygmaeus* Zone, which is 20-25 m above the base of the Cincinnati in its reference area, corresponds to a level in the middle part of the Cobourgian of New York.

Introduction

Two of the truly classical areas in the Ordovician regional geology of North America are north-central New York and adjacent parts of Ontario and Quebec, and the Cincinnati region of Ohio, Kentucky, and Indiana. These regions include the type areas for the Mohawkian Series and the Cincinnati Series, respectively, which are standard units in the classification of the North American Ordovician. The Mohawkian Series represents the upper Middle Ordovician, and the Cincinnati Series represents the Upper Ordovician (e.g., Ross et al., 1982).

The geological settings of these two regions differ in several important respects. The Mohawkian-type area is a part of the northern Appalachian Basin (Figure 1) and represents a foreland basin and the

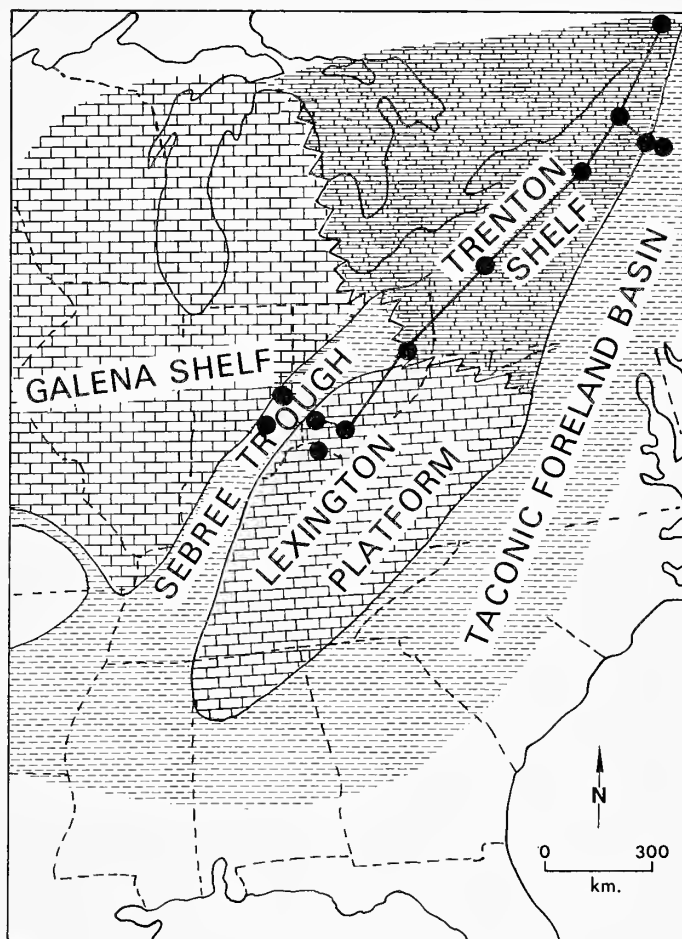


Figure 1. Sketch-map showing some major depositional regimes in eastern North America during late Mohawkian (late Middle Ordovician) time (modified from Keith, 1985). Black dots show location of some of the sections discussed in the text. For section designations, see Figures 8 and 9.

adjacent shelf. Numerous outcrops illustrate the striking facies change from basinal shales in the east to shelf carbonates in the west and northwest. The Cincinnati region has a cratonic setting on the northwestern portion of the Lexington Platform (Figure 1), where most of the Cincinnati Series and subjacent Middle Ordovician strata consist of shallow-water carbonates. The Lexington Platform is bordered on the

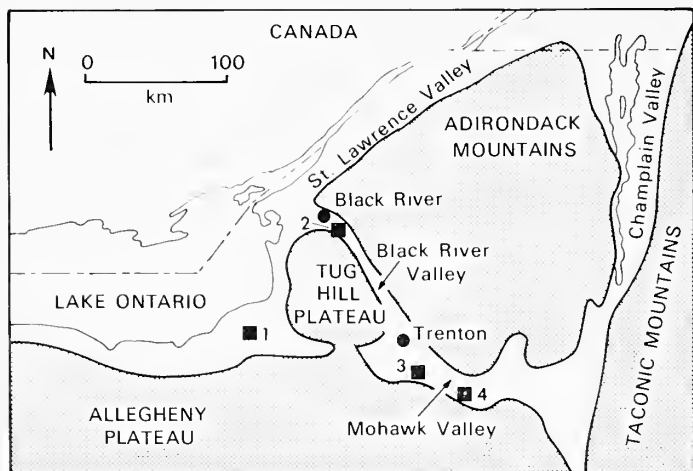


Figure 2. Schematic map of north-central New York showing location of Black River and Mohawk valleys and some sections referred to in the text. 1, House well, Oswego County; 2, Lowville, Lewis County; 3, Nowadaga and adjacent creeks, Herkimer County; 4, Canajoharie, Montgomery County (modified from Bergström, 1986).

northwest by the Sebree Trough, a sublinear feature more than 900 km long that extends from central Ohio to western Tennessee. It is characterized by deeper-water fine siliciclastic sediments that differ markedly in their lithology from adjacent, coeval Lexington Platform deposits. Northwest of the Sebree Trough is the vast Galena Shelf with dominant shallow-water carbonates that can be traced into the upper Mississippi Valley. These carbonates are the reservoir rocks of the prolific Trenton oil fields in Ohio, Indiana, and Michigan.

Interpretation of the relations between the upper Middle and lower Upper Ordovician successions in the Mohawkian- and Cincinnati-type areas has been hampered by the lack of exposure of these rocks in eastern and northern Ohio, much of Pennsylvania, and western New York. Rickard (1973) used geophysical logs to trace Mohawkian and lower Cincinnati rocks in the subsurface through much of New York and adjacent areas, but his work did not extend as far as Ohio, and fossils were not used to establish stratigraphical relationships. Nevertheless, Rickard's (1973) study is a major contribution that reveals some significant stratigraphical relations.

The purpose of the present research is to examine whether or not it is possible to use geophysical and other logs in conjunction with bio-

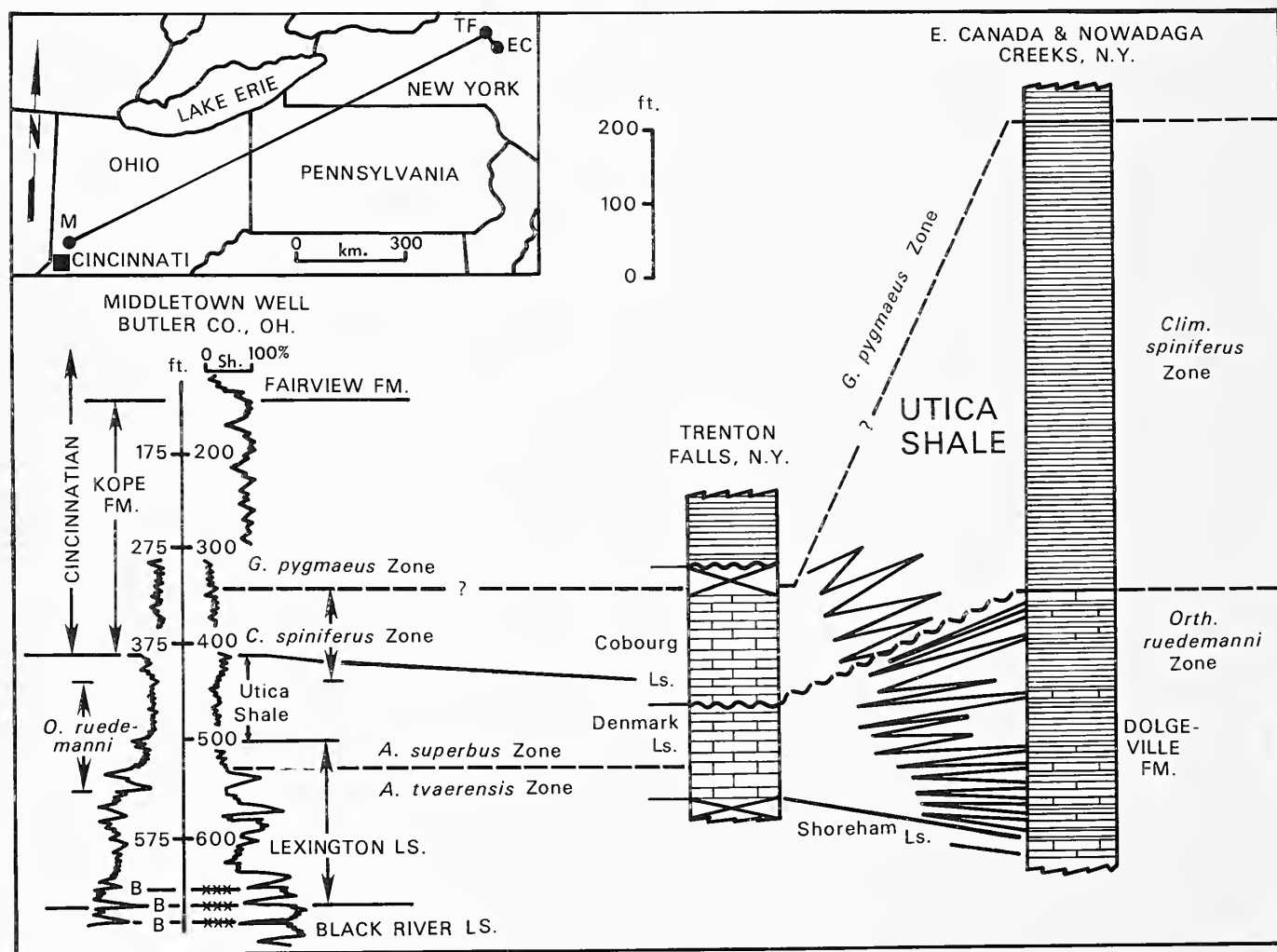


Figure 3. Stratigraphic relations between key successions in southwestern Ohio and Trenton Falls and the Mohawk Valley, New York, as suggested by graptolite and conodont biostratigraphy. Relations between the Canajoharie and Trenton Falls successions follow Rickard (1973). The base of the *Climacograptus spiniferus* Zone in the Middletown well is tentatively defined at the level of disappearance of *Orthograptus ruedemanni*. Note facies change from the deeper-water sections in Mohawk Valley to the shallower-water succession at Trenton Falls. The letter "B" denotes K-bentonite beds near the Black River-Lexington contact in the Middletown well. For the occurrence of K-bentonites in the New York sections, see Figure 9.

stratigraphical and other evidence to clarify upper Middle and lower Upper Ordovician facies transitions from New York and Quebec to the Cincinnati region, a distance of about 1400 km. Such a study, if successful, would also provide useful new data on the precise relations between the top of the type Mohawkian Series and the base of the type Cincinnati Series, a much-discussed and somewhat controversial problem (Walters et al., 1982; Sweet, 1984, 1988; Bergström and Mitchell, 1986; Mitchell and Bergström, In press). This report is dedicated to D.W. Fisher in recognition of his important contributions to our knowledge about Ordovician geology in North America.

The New York succession

The key sections of the Mohawkian Series are located in the Mohawk Valley–Black River Valley region south and southwest of the Adirondack Mountains in north-central New York (Figure 2). In the Mohawk Valley, most of the Mohawkian consists of graptolite-bearing, dark basinal shale, referred to as the Utica Shale (e.g., Fisher, 1977). These shales belong to a huge clastic wedge that can be traced eastward into the Taconic area in easternmost New York and adjacent Vermont. The Utica Shale contains four standard graptolite zones: the *Corynoides americanus*, *Orthograptus ruedemanni*, *Climacograptus spiniferus*, and *Geniculograptus pygmaeus* Zones (Figure 3). For a discussion of the faunas and distribution of these zones, see Riva (1969, 1972).

The Utica Shale of the Mohawk Valley grades westward into a mixed limestone–shale facies, the Dolgeville Formation, which has been interpreted to represent a shelf-slope deposit (Cisne et al., 1982). To the northwest and west, the Dolgeville Formation grades into the partly peritidal, dark grey carbonates of the Trenton Group (Figure 3), which are widely distributed and well-exposed in the Black River valley and adjacent areas to the north and northwest. The latter unit is

named for magnificent exposures at Trenton Falls (Kay, 1937), but the term *Trenton Limestone* has been used uncritically for lithologically quite different, but broadly coeval, limestones over much of the eastern Midcontinent, especially in subsurface stratigraphy. At Trenton Falls and elsewhere southwest and west of the Adirondack Mountains, the Trenton Group limestone succession is overlain, at most localities unconformably, by the uppermost part of the Utica Shale with graptolites of the *Geniculograptus pygmaeus* Zone (Figure 3). Recent tracing of K-bentonite beds from the eastern shale facies into the western shelf carbonate facies has provided partial confirmation of previously inferred stratigraphical relationships (Cisne et al., 1982; Trippi, 1986; Goldman et al., 1991). This confirmation is important because the biostratigraphically significant graptolites in the Utica Shale are not known from the Trenton Group, and the Trenton Group conodont and shelly fossil biostratigraphy (Kay, 1937; Schopf, 1966; Fisher, 1977; Titus, 1982, 1986) cannot be applied to the Utica Shale because of biofacies differences.

The Trenton Group–Utica Shale succession represents a transgression from the east or southeast that was probably related to initiation of tectonic activity during an arc-continent collision (Bird and Dewey, 1970; Cisne et al., 1982). As shown by regional facies relations, paleo-current directions (Cisne et al., 1982), and increase in grain size toward the east, the source area of the fine clastic material of the Utica Shale was to the east, presumably from rising highlands formed by Taconian orogenic activity.

In terms of regional Middle and Late Ordovician biostratigraphy, the composite shale–carbonate succession in New York State is important not only because it is a classical reference standard, but also because it is one of the few sections of that age in North America, and indeed in the entire world, where evidence from several key index fossil groups can be integrated with some precision. This correlation is illustrated schematically in Figures 3 and 4.


SERIES		CINCINNATI REGION	NEW YORK	GRAPTOLITE ZONES	CONODONT ZONES		
					ATLANTIC	MIDCONTINENT	
Upper Ordovician	Cincinnatian			<i>D. complanatus</i>	<i>A. ordovicianus</i>	<i>A. shatzeri</i>	
		Richmondian				<i>A. divergens</i>	
		Maysvillian		Cobourgian	<i>A. manitoulinensis</i>	<i>A. superbus</i>	<i>A. grandis</i>
		Edenian					<i>O. robustus</i>
Upper M. Ordovician	Mohawkian		Cobourgian	<i>G. pygmaeus</i>	<i>A. superbus</i>	<i>O. velicuspis</i>	
				Shermanian		<i>C. spiniferus</i>	<i>B. confluens</i>
			Kirkfieldian	<i>O. ruedemanni</i>	<i>A. tvaerensis</i>	<i>P. tenuis</i>	
			Rocklandian	<i>C. americanus</i>		<i>P. undatus</i>	
				<i>C. bicornis</i>			

Figure 4. Correlation of Middle and Upper Ordovician series, stages, graptolite, and conodont zones based on the New York and Ohio successions (modified from Bergström, 1986).

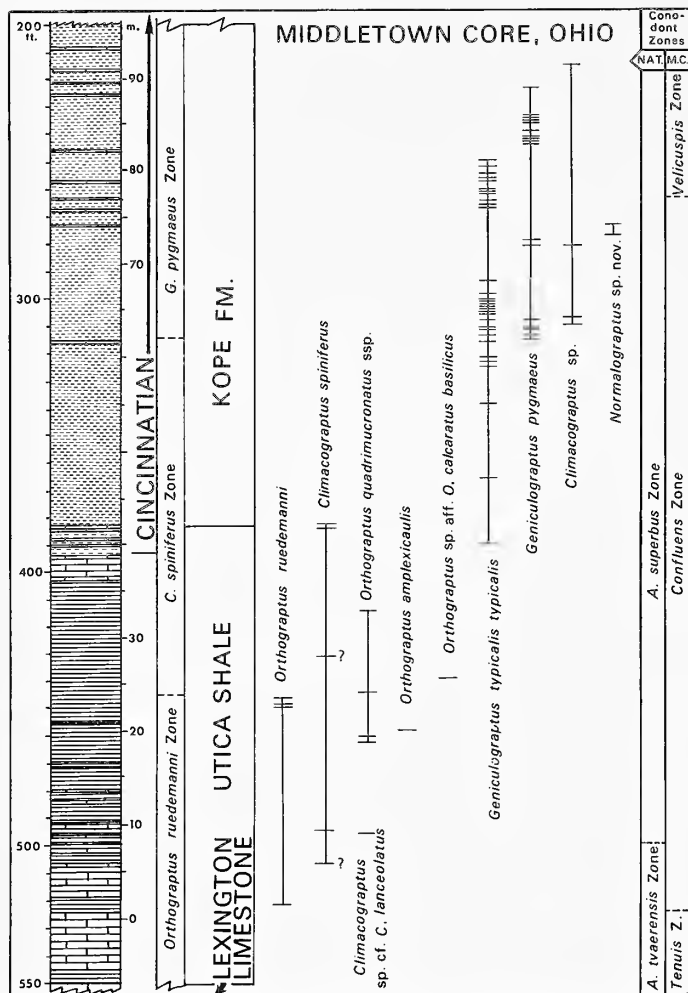


Figure 5. Ranges of graptolite species in the upper Mohawkian and lower Cincinnatian of the Middletown core, Butler County, Ohio. Note the relations between the base of the Cincinnatian and the graptolite zone succession. The base of the *Climacograptus spiniferus* Zone is tentatively drawn at the top of the range of *Orthograptus ruedemanni* (slightly modified from Mitchell and Bergström, In press).

The Cincinnati region succession

The upper Middle and Upper Ordovician in the Cincinnati region consists of richly fossiliferous limestones, shales, and mudstones deposited in epicontinental shallow-water environments on the northwestern portion of the Lexington Platform (Figure 1). These rocks and their diverse faunas have been the subject of much study since the early 19th century, but recent investigations have produced much new information. Such investigations have dealt with depositional environments and lithologies (for a recent summary, see Meyer et al., 1981) and biostratigraphy (Sweet, 1979, 1988; Mitchell and Bergström, In press).

The succession dealt with herein includes, in ascending order, the Lexington Limestone, the Utica Shale, the Point Pleasant Formation, and the Kope Formation (Figures 5 and 6). Following long-standing practice, the base of the Kope Formation at Cincinnati is taken to be the base of the Cincinnatian Series. No reference section has been formally selected for the Cincinnatian Series, nor is there a designated type locality for the base of the Series in the Cincinnati region. The base of the Series is not exposed in the type area and is now below the level of the Ohio River as a result of dam construction during the last century

(Bergström and Mitchell, 1986).

The Lexington Limestone rests on intertidal to shallow-subtidal, mostly calcilitic limestones of Black Riverian age, and represents the beginning of a transgressive period in the Cincinnati region. It is dominantly a limestone unit, but the overlying Point Pleasant Formation consists of interbedded shales and limestones. The transgression culminated in the deposition of the Kope Formation, which is mainly shale and mudstone with subordinate limestone interbeds. The Lexington Limestone and the Point Pleasant Formation contain several laterally persistent K-bentonite beds that have proved useful for local correlation (Stith, 1986; Schumacher and Carlton, 1989).

As noted above, there is a rather narrow belt (Figure 1), referred to as the "Sebree Trough" (Bergström and Mitchell, 1987, 1990), of deeper-water dark brown to grey shales and mudstones along the northwestern side of the Lexington Platform. These rocks (Utica Shale of drillers), which contain abundant graptolites (Bergström and Mitchell, 1990) but lack a benthic fauna, are known only from the subsurface, and appear to interfinger with the Lexington Limestone of the Lexington Platform (Figures 5-7). The Sebree Trough appeared as a distinctive depositional area in post-Black Riverian time (Keith, 1985, 1989) and ceased to exist in early Cincinnatian time, when the Utica Shale was blanketed by late Edenian light grey shales and mudstones (Mitchell and Bergström, In press). The cause of the formation of the Sebree Trough remains uncertain, but the data now available suggest that it is neither a fault graben nor associated with a known major tectonic feature.

The recently discovered graptolite faunas in the Utica Shale of the Sebree Trough (Bergström and Mitchell, 1986, 1990; Mitchell and Bergström, 1987, In press) are virtually identical with those in the Utica Shale of the Mohawk Valley and permit correlation with Riva's (1969) standard zonal succession in New York and Quebec. In addition, investigations of graptolites in drill cores from the southeastern flank of the Sebree Trough (Figures 5, 6) and in surface sections in the Cincinnati region have made it possible to trace some graptolite zones into the Lexington Platform shelly succession (Mitchell and Bergström, 1988, In press). This is of considerable significance for the regional correlation of the upper Mohawkian and lower Cincinnatian and the base of the Cincinnatian Series.

Methods

In the present study, several types of information have been used to establish stratigraphic relationships. These include gamma-neutron and shale percentage logs, conodont and graptolite biostratigraphy, distinctive lithologic changes, and regionally traceable K-bentonite beds or complexes of such beds.

The usefulness of geophysical logs for tracing Mohawkian and lower Cincinnatian rocks in the subsurface of New York and nearby areas was demonstrated by Rickard (1973), and similar work has subsequently been carried out in southern and southwestern Ohio (Stith, 1986). Rickard's (1973) tracing of distinctive markers in geophysical logs has been accepted with minor modifications in the present study because most of his conclusions agree with our biostratigraphic framework. By the use of logs from areas not covered by Rickard (1973), his work has been extended from western New York to southwestern Ohio. In the latter area, shale-percentage logs (Weiss et al., 1965; Sweet et al., 1974) have also been used in this study.

Rickard's (1973) conclusion that detailed comparison of geophysi-

cal logs makes it possible to trace relatively thin stratigraphic units for hundreds, or even thousands, of kilometers is accepted herein. Biostratigraphic data, as well as time-planes provided by distinctive and regionally traceable K-bentonite beds or complexes of such beds, suggest strongly that most of the geophysical log markers are synchronous from well to well, and that rock packages of surprising uniformity can be traced over considerable distances. It is of interest to note that Templeton and Willman (1963) arrived at a similar conclusion based on lithological tracing of Middle Ordovician rocks that crop out in other parts of the Midcontinent region.

Regional work has led to the establishment of refined conodont biostratigraphy in the Mohawkian and Cincinnati in both the Midcontinent region and the Appalachians (Schopf, 1966; Bergström and Sweet, 1966; Sweet and Bergström, 1971, 1976; Sweet, 1979, 1984, 1988; Bergström, 1971a, 1971b; Bergström et al., 1988). A significant advance in these studies is the development of a conodont-based graphic correlation scheme and zonal succession by Sweet (1984, 1988), which has been applied to the sequence in several key outcrop areas in the eastern Midcontinent region. It has also been tied to the Atlantic standard conodont zone scheme of Bergström (1971a, 1983). In the present study, the latter scheme is mainly used because much of the detailed faunal evidence employed in developing the graphic correlation scheme has not yet been published, and most of the sections dealt with herein have not been included in the graphic correlation network. A correlation between graptolite zones and Midcontinent and Atlantic conodont zones is presented in Figure 4.

In recent years, considerable progress has been made in clarification of the biostratigraphy and taxonomy of Mohawkian and Cincinnati graptolites in New York State and Quebec (Riva, 1969, 1972, 1976; Riva and Malo, 1988; Walters, 1977; Walters et al., 1982) and in the Cincinnati region (Bergström and Mitchell, 1986, 1990; Mitchell and Bergström, In press). In this report, Riva's (1969, 1972) graptolite scheme is used, but the definitions of his *Corynoides americanus* and *Orthograptus ruedemanni* Zones are clearly in need of reappraisal. The new generic designations and other taxonomic changes proposed by Mitchell (1987) have also been adopted here.

The use of major lithological changes as stratigraphic guide horizons is limited in this report because some of these changes, such as the contact between the Trenton Group carbonates and the Utica Shale clastics, are clearly markedly diachronous (Figure 7), or may represent unconformities. Other lithologic changes, such as that at the base of the Lexington Limestone, appear to be synchronous, or nearly so, at least within a geographically restricted area (Figure 6).

Successful use of K-bentonite beds as event-stratigraphic markers in the Ordovician of the Midcontinent region has been repeatedly documented in recent years (Cisne et al., 1982; Bergström, 1982, 1990; Kolata et al., 1986; Cullen-Lollis and Huff, 1986; Huff et al., 1988; Huff and Kolata, 1990). The thick K-bentonites, such as the Deicke and the Millbrig (Kolata et al., 1986), can readily be traced regionally with a high degree of confidence. Less prominent beds, even if they are not present in every section, may also be useful chronostratigraphically. However, it must be stressed that control by biostratigraphy (Bergström, 1982, 1990) or chemical fingerprinting of ashes (Cullen-Lollis and Huff, 1986) is essential for establishment of reliable relations between individual beds in sections that are separated by a substantial geographic distance. In the present study, it is concluded that the Deicke and several other K-bentonite beds, or complexes of beds, can be traced over long distances with a high degree of confidence.

The New York–southwestern Ohio cross section

Figure 7 illustrates the interpretation of the stratigraphical relations in the upper Mohawkian and lower Cincinnati in a cross-section that extends from Lewis County, New York, to Butler County, Ohio. Apart from the Lewis County section, all the figured sections are based on wells. An attempt was made to select wells that were spaced at relatively regular geographic intervals and for which good logs and, preferably, other stratigraphic controls, were available.

The following observations and comments can be made about Figure 7:

1. The prominent K-bentonite beds (including the Deicke and the Millbrig) in the Black Riverian–Rocklandian boundary interval are recognizable in most wells, and they are excellent marker beds. With the exception of the Shaw well in Pennsylvania, these K-bentonite beds are present near a conspicuous lithological change from dominantly calcilititic to dominantly calcarenitic limestone. It is likely that this regional change was brought about by a deepening of the depositional environment over much of the eastern Midcontinent region.
2. The *Amorphognathus tvaerensis*–*Amorphognathus superbus* conodont Zone boundary, which is based on a speciation event in a well-documented evolutionary lineage (Bergström, 1971a), is near the top of the Lexington Limestone in the Middletown well and in the lower part of the Denley Limestone in New York (Bergström, 1971b). Tracing of K-bentonite beds in the Mohawk Valley shows that this level corresponds to a horizon in the *Orthograptus ruedemanni* Zone (Figures 3 and 4). The stratigraphic interval between the top of the Black Riverian sequence and the base of the *Amorphognathus superbus* Zone is about 40% thicker in the Trenton Group in New York than in the Lexington Limestone of southwestern Ohio (Figure 7). This difference compares with a difference of about 30% in the thickness between the top of the Black Riverian sequence and the base of the Cincinnati Series between these areas. Evidently, the relative rate of carbonate net accumulation during Mohawkian time was higher in New York than in the Cincinnati region.
3. The Utica Shale of the Seabee Trough (Mitchell and Bergström, In press; Figure 5), can be traced into an interval of interbedded shale and limestone that is called the Point Pleasant Formation (Stith, 1986) in southern and eastern Ohio. This interval loses its lithological distinctiveness when traced into Pennsylvania (Figure 7) but appears to correspond, at least in part, to an interval of dark calcareous shale with some interbedded limestones called the Salona Formation by Wagner (1966). No fossil control is available from this well, but, provided the proposed correlation is correct, the Point Pleasant Formation of Ohio is also coeval with a lithologically undifferentiated portion of the Denley Limestone in the Trenton–Black River region of New York.
4. The Kope Formation can be traced through southern and eastern Ohio into the Marshall well. However, the marked facies change from the grey, highly calcareous shales of the Kope Formation of this well into the black, weakly calcareous Utica Shale in the Shaw well makes detailed gamma-neutron log correlation difficult, if not impossible. Based on general stratigraphic relations, and assuming that there is not a major unconformity at the base of the Utica Shale in the latter well, the lower part of the Kope Formation is correlated with a portion of the Utica Shale, which reaches a thickness of 107

m in this well (Wagner, 1966). Farther to the east, the lower part of the Utica Shale grades into Cobourgian limestones, which are overlain by the upper part of the Utica Shale with graptolites of the upper *Geniculograptus pygmaeus* Zone. The cross section suggests that the Kope Formation corresponds to a major part of the Cobourgian in New York.

5. On the basis of this tentative correlation, the *Climacograptus spiniferus*–*Geniculograptus pygmaeus* graptolite Zone boundary, which has been traced in subsurface and surface sections in southwestern Ohio (Mitchell and Bergström, In press), should correspond to a horizon in the middle part of the Cobourgian, perhaps in the Steuben Limestone or somewhat lower. Regrettably, this portion of the Trenton Group has not produced zonally diagnostic graptolites. Correlation of the Kope Formation of Ohio with much of the New York Cobourgian is supported by the fact that the *Amorphognathus superbus*–*A. ordovicicus* Zone boundary, which is in the middle to upper Maysvillian of Ohio, has been identified in the uppermost Hillier Limestone in New York (Bergström, 1971b). On the basis of

the graptolite biostratigraphy in the Cincinnati region (Bergström and Mitchell, 1986) and on Manitoulin Island, Ontario (Bergström, unpublished data), this level is in the uppermost part of the *Geniculograptus pygmaeus* Zone, or in the lowermost part of the *Amplexograptus manitoulinensis* Zone.

6. The Shorehamian–Denmarkian K-bentonite bed complex in the Mohawk Valley–Black River region has its counterpart in Pennsylvania, although bed-by-bed correlation is difficult. This K-bentonite bed complex is not well developed in southern and southwestern Ohio, but one bed 3–6 m below the top of the Lexington Limestone and another 12–15 m above the base of the Point Pleasant Formation have been identified in several wells (Schumacher and Carlton, 1989). These K-bentonites appear to correspond to two of the beds in the Denmarkian part of the *Amorphognathus superbus* Zone in the Trenton Group.
7. The level taken as the base of the Cincinnati Series in the Middletown well, which was drilled at a site about 50 km NNE of Cincinnati, seems to correlate with a level in the basal 5–10 m of the

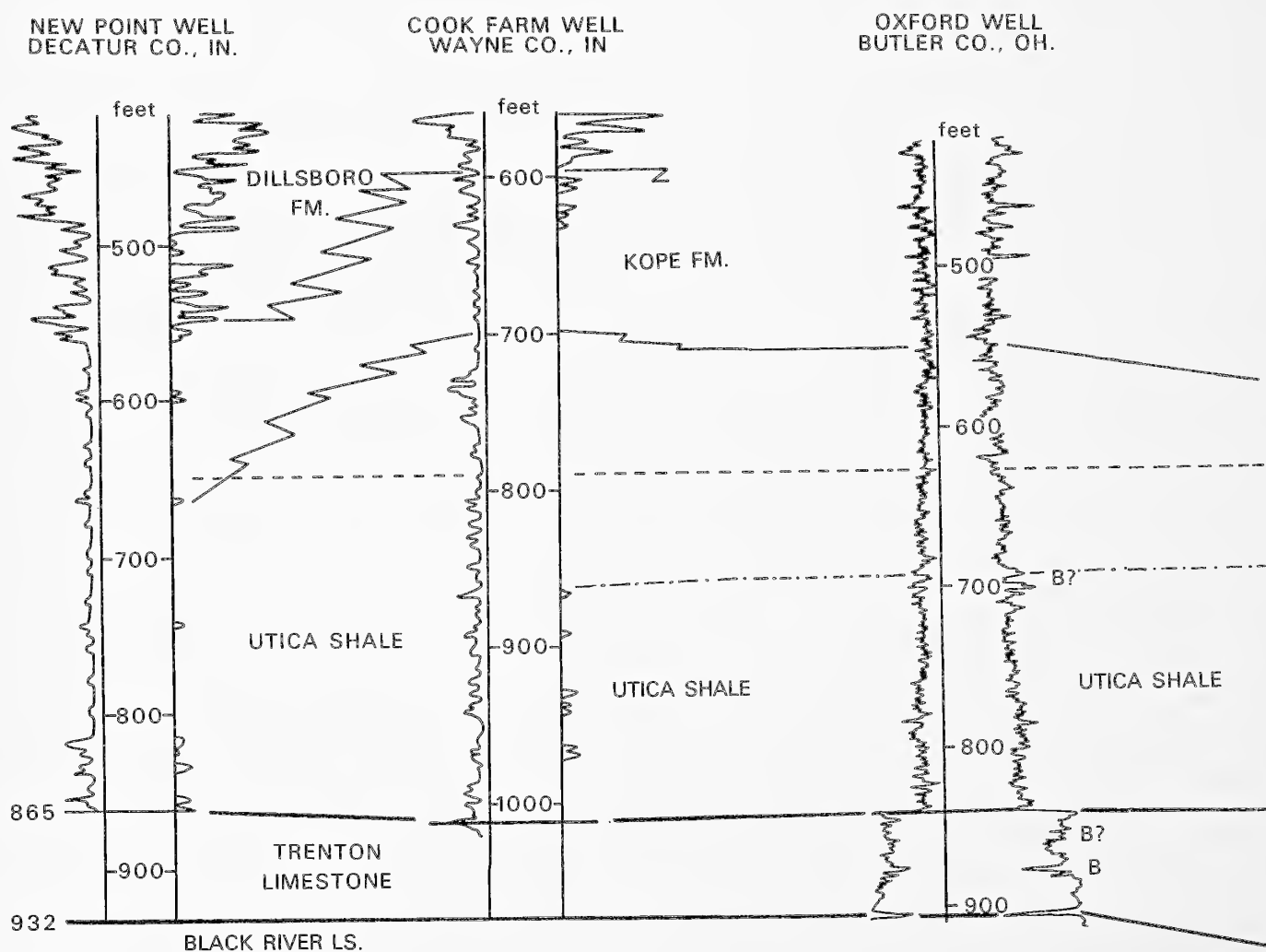


Figure 6. Cross-section from easternmost Indiana to the Cincinnati region showing relations between the Utica Shale in the Sebree Trough and the Lexington Platform succession. Note position of the *C. spiniferus*–*G. pygmaeus* zonal boundary (modified from Mitchell and Bergström, In press).

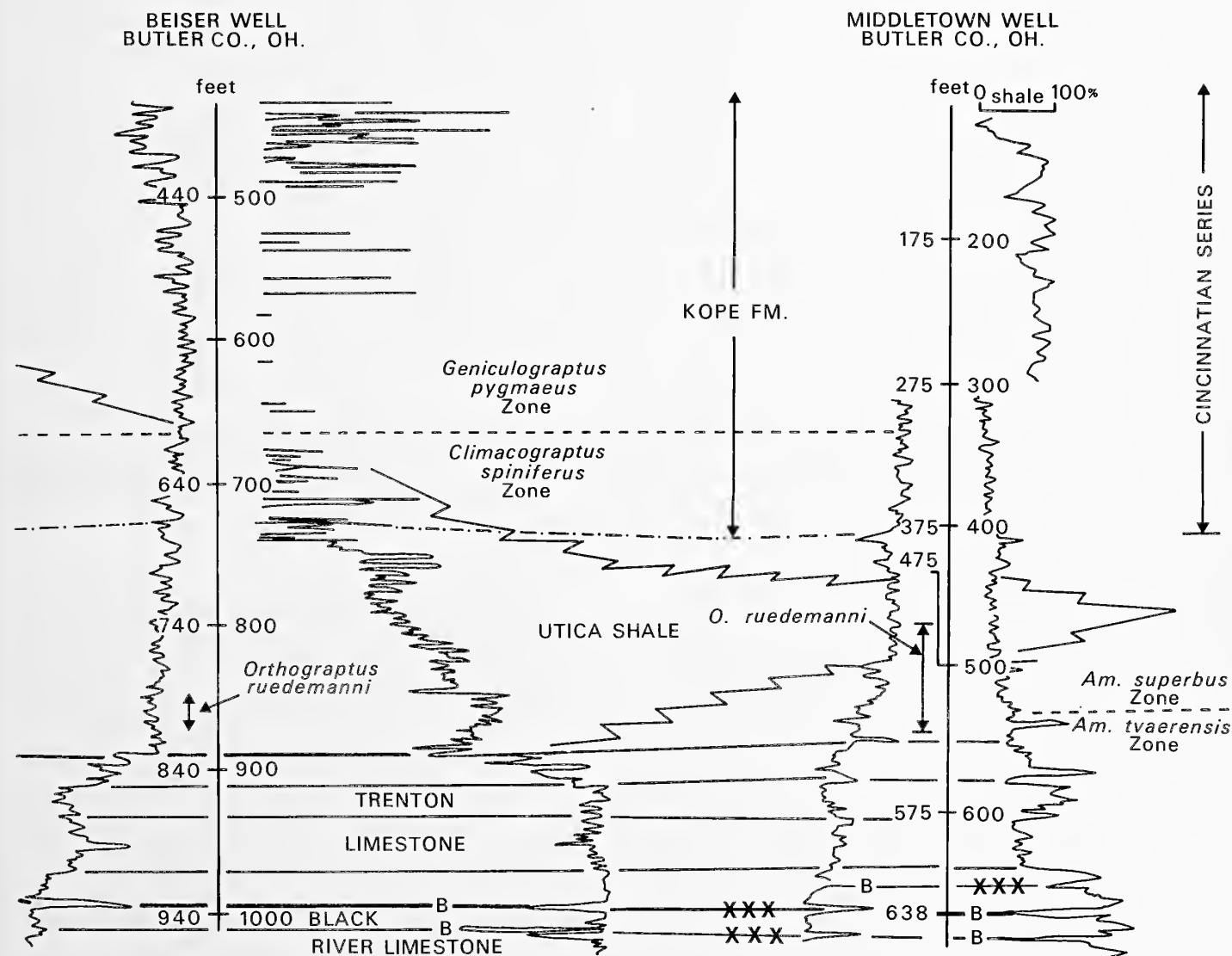
Cobourgian. This level is slightly higher than, but in broad agreement with, previous correlations based on conodont evidence (Sweet and Bergström, 1971; Sweet, 1984).

8. As shown in Figure 7, the Mohawkian succession is relatively uniform in wells across southern Ohio and between western Pennsylvania and New York State. However, there is a prominent change between the Marshall and Shaw wells, and as indicated above, correlation between these wells is somewhat problematic. This change is in the border region between the Lexington Platform and the Trenton Shelf (Figure 1), but further studies are clearly needed to establish the cause and nature of this transition.

The New York-Quebec cross section

Figure 8 illustrates the interpretation of upper Mohawkian and lower Cincinnati stratigraphic relations in a cross-section from Oswego County, New York, to easternmost Ontario, and from there across the St.

Lawrence Lowlands to Neuville, southwest of Quebec City. This cross-section is based on wells that have been correlated previously by Rickard (1973), but new details are added and slight modifications of some of his correlations are proposed. In terms of regional stratigraphical relations, the results presented here do not differ substantially from those of Rickard (1973), but extensive graptolite work published largely after 1973 has improved the biostratigraphic control (Walters, 1977; Belt et al., 1979; Walters et al., 1982; Riva and Malo, 1988). Although derived mostly from sections other than those illustrated in Figure 8, this graptolite information is important for assessment of regional stratigraphic relations, and it has been fully considered in the interpretation. Little useful information is available from other fossil groups represented in the upper Mohawkian and lower Cincinnati in the St. Lawrence Lowlands. Most of the conodont data published by Globensky and Jauffred (1971) were based on now-outdated form taxonomy and are difficult to interpret. Shelly fossils are common in some of the carbonate units, but the available distribution data are not useful for biostratigraphic purposes. Extensive chitinozoan work in eastern Canada by Achab (1989), and



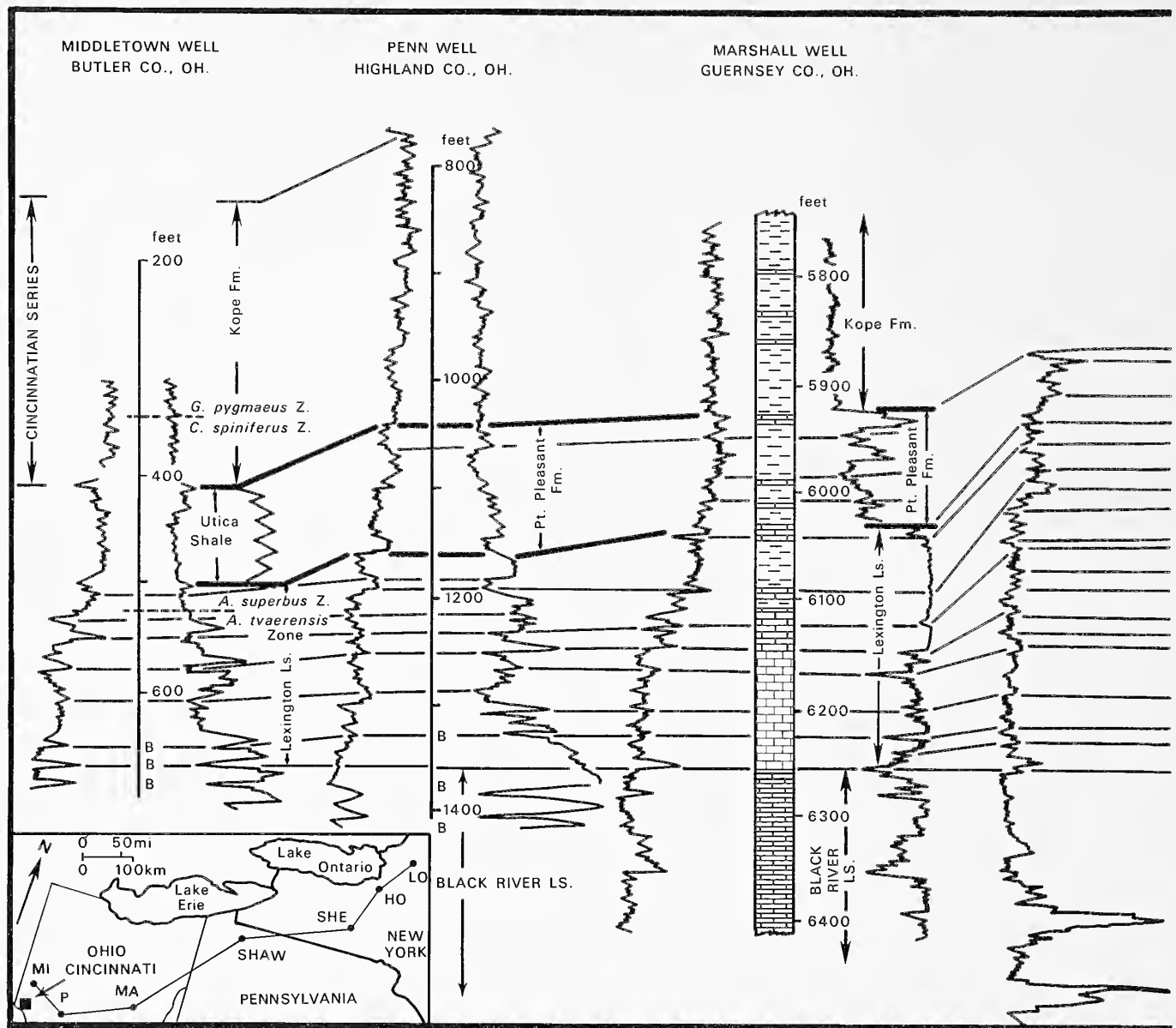


Figure 7. Cross-section from Butler County, Ohio, to Lewis County, New York, showing proposed correlation based on tracing of gamma-neutron log markers, conodont and graptolite zones, and K-bentonite beds. Letter "B" within circle is K-bentonite horizon; letter "B" (not circled) is level of K-bentonite projected from adjacent section. In the Penn well, the K-bentonite levels are projected from several wells in southwestern Ohio (Schumacher and Carlton, 1989; D.A. Schumacher, personal communication, 1988); those in the Shaw well are from the Kardosh well about 67 km to the west (Wagner, 1966); those in the Shephard well

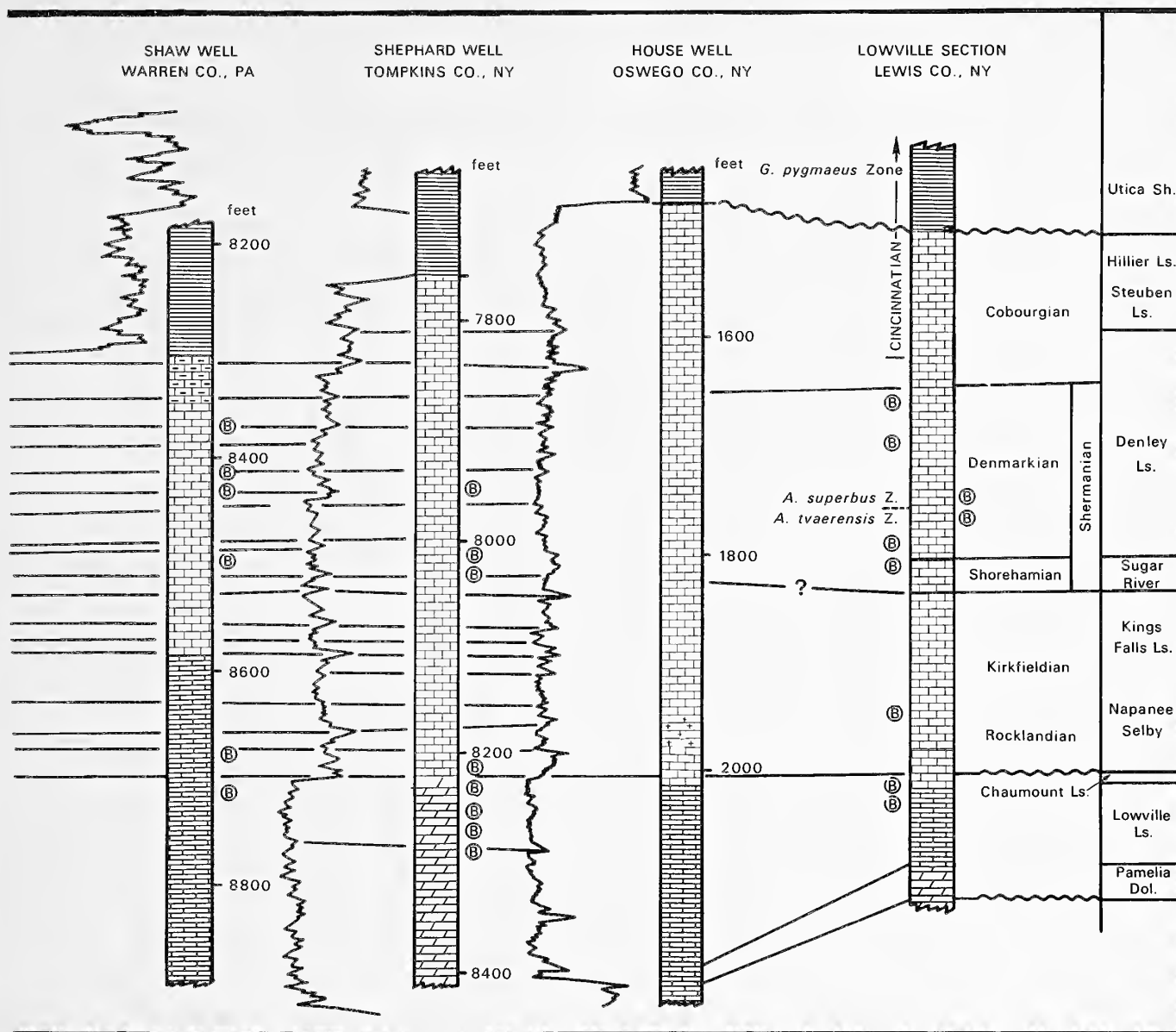
Martin's (1983) chitinozoan and acritarch investigations, were partly based on samples from the upper Mohawkian and lower Cincinnatian of the St. Lawrence Lowlands. Although important, neither of these studies contains biostratigraphical data useful for evaluation of the stratigraphical relations between the successions illustrated in Figure 8.

On the basis of Figure 8, the following comments and conclusions can be made:

1. As has been noted previously by Rickard (1973), rocks coeval with the New York Black River Group decrease in thickness toward the northeast across the St. Lawrence Lowlands, and pinch out between Montreal and Quebec City (between the IMP-Low 2 and Neuville wells in Figure 8). At Neuville, the Trenton Group equivalents rest nonconformably on the Precambrian.
2. The post-Black Riverian limestone succession has a closely similar thickness from north-central New York (House well) to easternmost

Ontario (Consumers 16308 well), a distance of more than 200 km. A considerable number of markers on the geophysical logs can be traced between these wells, and it is concluded that these levels are, in all likelihood, isochronous surfaces. Regrettably, there is no fossil control in these wells, but the log correlations suggest that the Tetraeuville Formation of easternmost Ontario is essentially equivalent to the Cobourgian of north-central New York.

3. The Tetraeuville Formation becomes increasingly shaly northeastward. Its lower part grades into the Utica Shale, and its upper part into the Lotbinière Formation between Montreal and Quebec City (Belt et al., 1979). This facies change is accompanied by an increase in thickness. Interestingly, the thickness of the post-Black Riverian carbonate succession in easternmost Ontario is virtually the same as that of the limestone succession at Neuville. Northeast of Quebec City, the late Mohawkian sequence (Lotbinière Formation, etc.) consists of distal flysch, sandstone, and shale of considerable thickness.

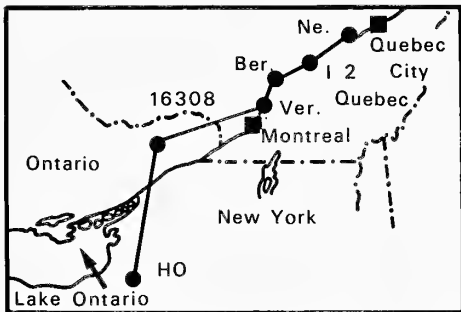


are from the Kesselring well about 21 km to the south (Wagner, 1966); and those in the Lowville sections are from outcrops in the Black River-Trenton area (Kay, 1935, 1937; Templeton and Willman, 1963; Bergström, 1990). The lithologic successions in the wells are based on Rust (1961), Stith (1986), Calvert (1963), Wagner (1966), Rickard (1973), and unpublished data of S.M. Bergström and C.E. Mitchell.

Evidently, the source of the clastic material was the Taconian highlands, as was the case in coeval strata in the Mohawk Valley.

4. The proposed correlations between Montreal and Neuville are in full agreement with the graptolite biostratigraphy. When traced southwestward to Ontario and into New York, the Quebec graptolite zone boundaries match up well with the same zone boundaries that are traced northwestward from the graptolite shale sections in the Mohawk Valley.
5. In several of the Mohawkian successions in the St. Lawrence Lowlands, there are K-bentonite beds, some of which can be traced laterally over long distances. Brun and Chagnon (1979) reviewed the stratigraphic position and distribution of these beds, and their data have been used herein for regional comparisons. In most but not all cases, these beds are recognizable in the geophysical logs in Figure 8, and their vertical distribution pattern shows a surprising similarity to that of coeval units in New York about 500 km to the

southwest. Hence one bed (B1) in the uppermost Black Riverian Leray Formation in several sections between Ottawa and Berthierville is likely to be the very widespread Deicke bed (Huff et al., 1988), and has the stratigraphic position of one bed in the Chaumont Formation of New York (Kay, 1935). The proposed correlation of the late Mohawkian K-bentonites between Quebec and New York is illustrated in Figure 9. The B2 and B3 beds about 30 m above the base of the Mohawkian succession in the Quebec City area are at a closely similar stratigraphic level [within the *Corynoides americanus* Zone?] as the M2 and M3 K-bentonites above the Shoreham Limestone at Trenton Falls. The B4 bed is about 10 m above the base of the Montreal Limestone in the Ottawa area, and it occupies a stratigraphic position comparable to that of the M8 bed of Cisne et al. (1982) in the lower Denmarkian of Trenton Falls. The stratigraphic position of the B5 K-bentonite, which is about 40 m above the base of the Neuville Formation in the



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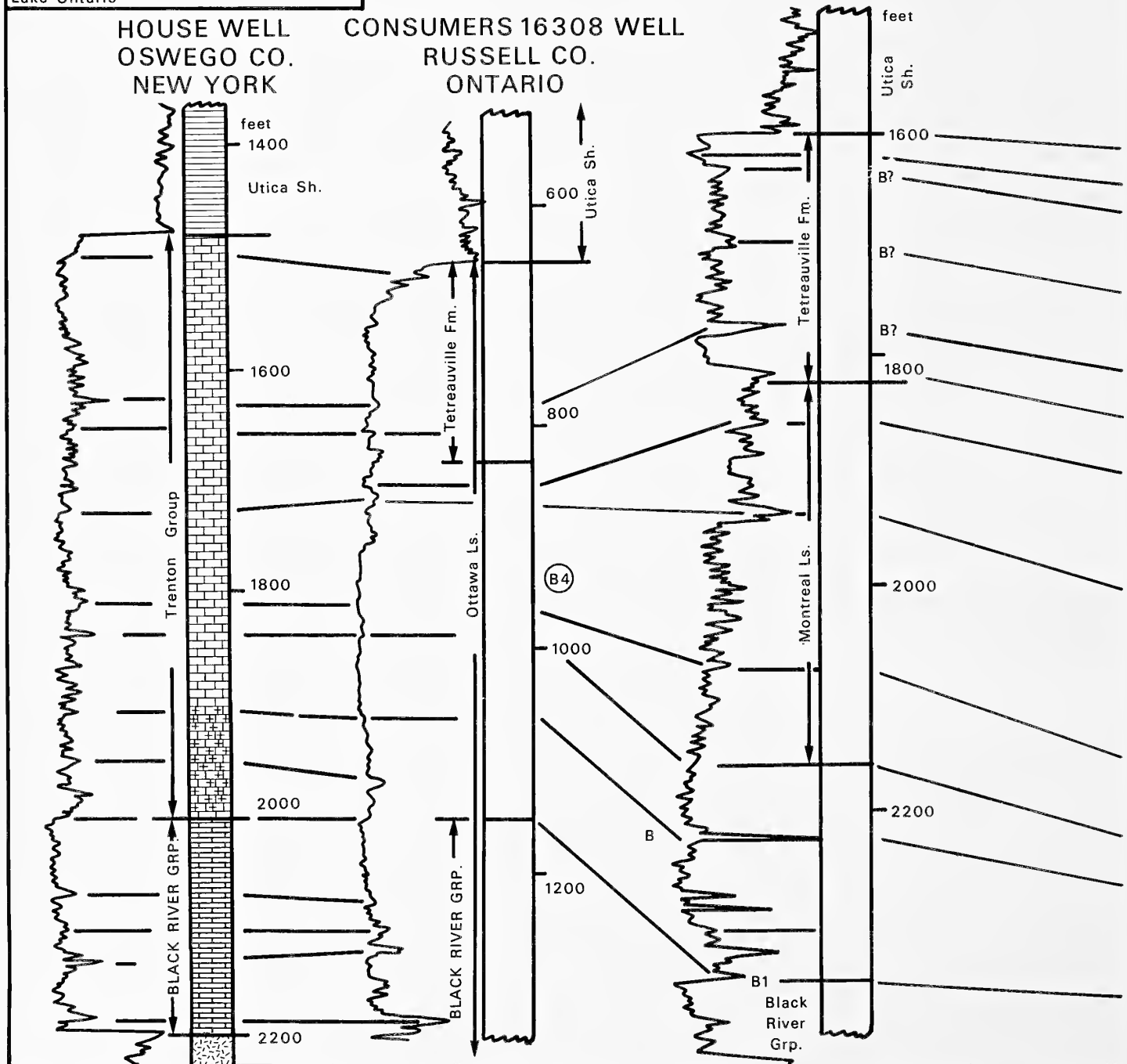
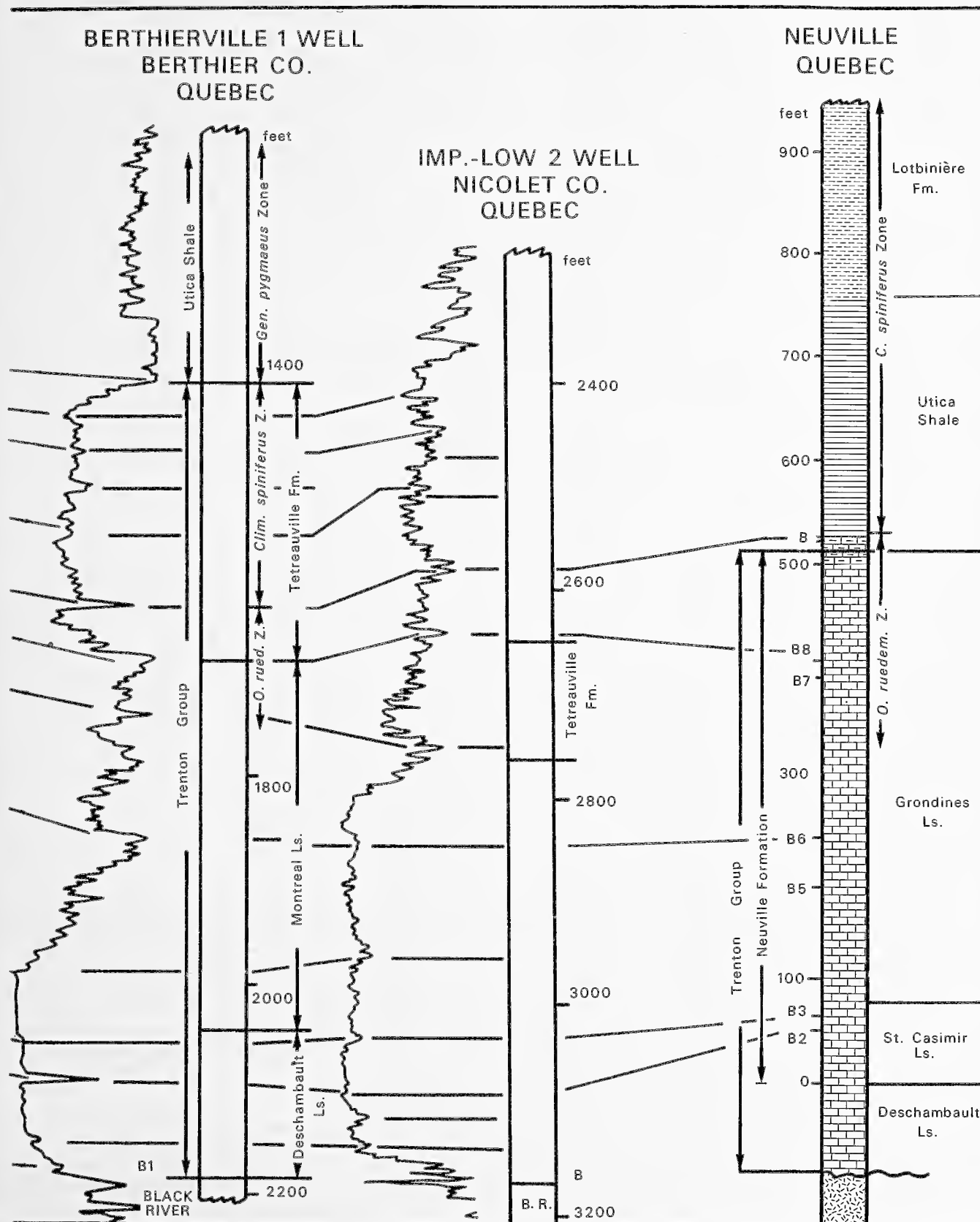


Figure 8. Cross section from Oswego County, New York, to Neuville, Quebec. After Rickard (1973) but with modifications and additions. Projected levels of K-bentonites after Brun and Chagnon (1979) and Belt et al. (1979). Graptolite zone boundaries after Riva (1969, 1972) and Riva and Malo (1988). Note that the upper



Trenton Group carbonate succession in New York-Ontario grades into dark shale facies with increase in thickness toward the northeast in the St. Lawrence Lowlands. All sections have the same vertical scale.

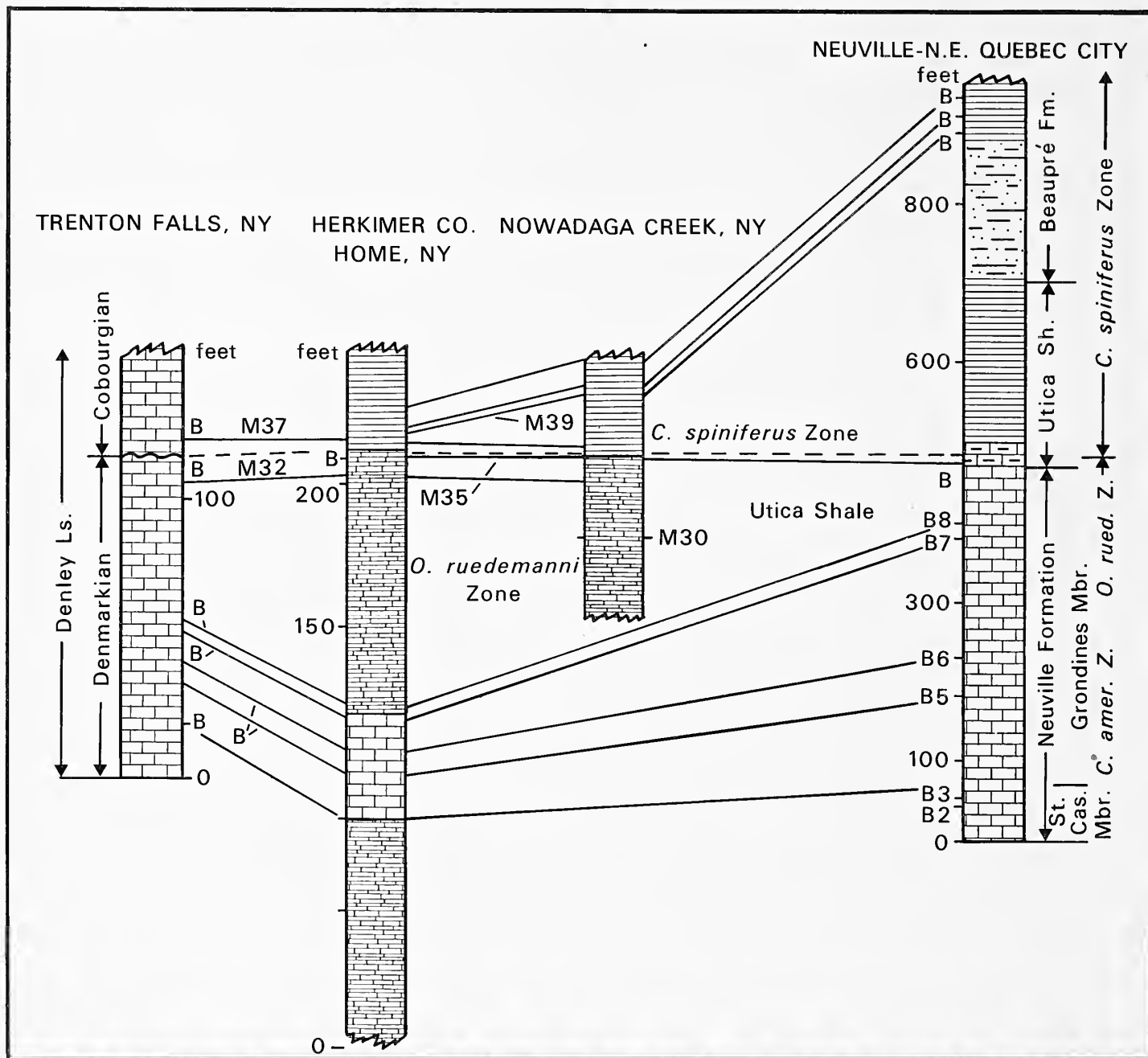


Figure 9. Correlation of K-bentonite beds between Neuville, Quebec, and three sections in the Mohawk Valley-Trenton Falls region, New York. Projected levels from Brun and Chagnon (1979), Belt et al. (1979), and D. Goldman (personal commun., 1991). K-bentonite designations in New York are based on figures in the composite standard succession of Cisne et al. (1982, fig. 4). Note the difference in vertical scale between the New York and Quebec sections.

Quebec City region, is similar to that of the B4 bed of the Ottawa region, and these beds may be coeval. The B6 bentonite, which is about 50 m above the base of the Neuville Formation in sections between Quebec City and Montreal, occurs at a stratigraphic level comparable to that of the M11 K-bentonite of Cisne et al. (1982) at Trenton Falls. The B7 and B8 beds are in the *Orthograptus ruedemanni* Zone, 95-100 m above the base of the Neuville Formation in the Neuville-Quebec City area, and their stratigraphic position is comparable to that of the widespread M15 and M16 beds in the Utica Shale of the Mohawk Valley and in the middle Denmarkian of Trenton Falls. Finally, the three K-bentonites recorded from the lower *Climacograptus spiniferus* Zone in the Beaupré Formation

northeast of Quebec City (Belt et al., 1979) could well be the same as the M38, M39, and M42 beds of Cisne et al. (1982) in the lower part of the same graptolite zone in the Utica Shale of the Mohawk Valley.

Concluding remarks

Figure 10 summarizes the interpretation of the upper Mohawkian-lower Cincinnati facies relations from the Lexington Platform in Ohio to the Trenton Shelf and the Taconian Foreland Basin in the St. Lawrence Lowlands and New York. For clarity, the detailed tracings of gamma-neutron log markers are not shown in this figure, but the position of sev-

eral levels that are interpreted to be isochronous horizons within the limits of our stratigraphic resolution are noted. These horizons include the following: (1) The Black Riverian–Rocklandian (Trentonian) boundary, which coincides with the Deicke K-bentonite (Sloan, 1987); (2) the *Amorphognathus tvaerensis*–*Amorphognathus superbus* conodont Zone boundary (Tv–Su); (3) the *Orthograptus ruedemanni*–*Climacograptus spiniferus* graptolite Zone boundary (Ru–Sp); and (4) the *Climacograptus spiniferus*–*Geniculograptus pygmaeus* graptolite Zone boundary (Sp–Py). As indicated in Figures 7 and 8, not all of these levels are yet identified in each of our sections, but the positions of those levels that are known are not in significant conflict with the correlations based on geophysical logs and K-bentonites. These various lines of evidence together form a rather tightly controlled stratigraphic framework.

Figure 10 illustrates some important regional aspects of the late Mohawkian and early Cincinnatian patterns of deposition from the interior platform to the foreland basin. Stages in the development of this pattern may be summarized as follows:

1. On the Lexington Platform and the Trenton Shelf, the Black Riverian rocks consist of very shallow-water, dominantly fine-grained carbonates that show remarkable horizontal uniformity. In both of the cross-sections, the Black Riverian succession pinches out eastward toward the edge of the foreland basin, but this is a local rather than a regional feature. Its local nature is shown by the fact that Black Riverian rocks are widely distributed and reach consider-

able thickness elsewhere in the Appalachian Basin.

2. Most of the overlying upper Mohawkian carbonates were deposited in somewhat deeper, but still relatively shallow, water during a period of a regional transgression, probably related to a eustatic change. The presence of numerous K-bentonite beds, especially in the successions of the foreland basin and the Trenton Shelf, indicates very active volcanism in a currently unknown area to the east. Although there is some facies differentiation, the platform and shelf successions are, by and large, relatively similar in lithology and thickness. However, they differ conspicuously from the contemporaneous siliciclastic sequences in the foreland basin. Several lines of evidence indicate that the source of these siliciclastics was to the east and from presumably uplifted areas near the marginal trench.

An important event during late Mohawkian time was the establishment of the Sebree Trough between the Galena and Lexington Platforms (Figure 1). It is possible that the development of this structure was associated with the formation of a peripheral bulge (Lexington Platform) adjacent to the Taconian Foreland Basin. Because the Sebree Trough was bordered on the east, northeast, and west by extensive carbonate terranes, it is likely that its siliciclastics had a different source area than those in the foreland basin; possibly the Sebree Trough clastics came from highlands to the south and southwest.

3. During early Cincinnatian time, the Sebree Trough ceased to exist as a distinct depositional basin, and the Lexington Platform and its sur-

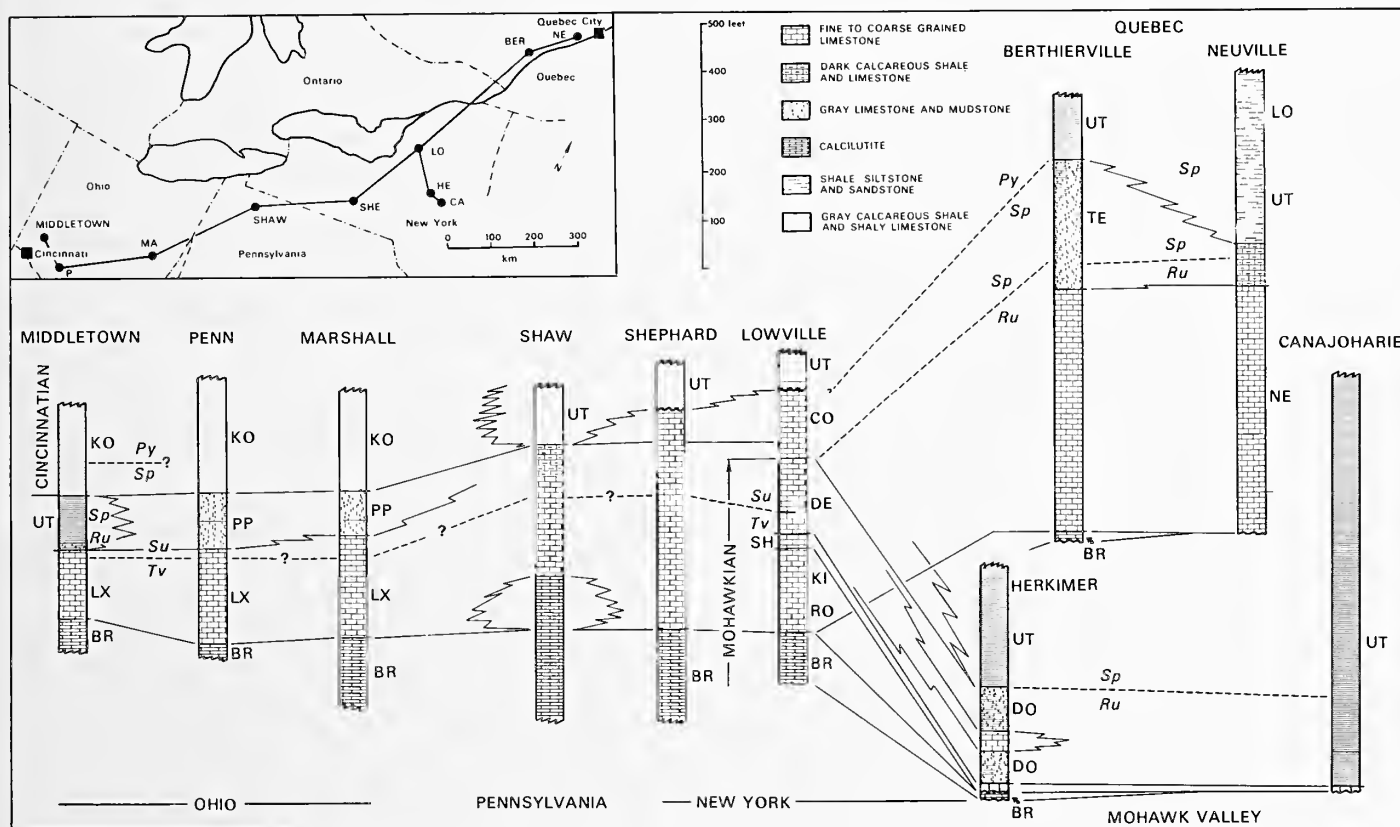


Figure 10. Summary diagram showing interpretation of stratigraphic relations and facies changes along cross-sections from southwestern Ohio to New York and the St. Lawrence Lowlands, Quebec. Figure is based on cross-sections illustrated in Figures 7 and 8. Broken lines mark faunal zone boundaries; solid lines, correlations based mainly on gamma-neutron logs. Su–Tv, *Amorphognathus superbus*–*Amorphognathus tvaerensis* Zone boundary (conodonts); Ru–Sp, *Orthograptus ruedemanni*–*Climacograptus spiniferus* Zone boundary (graptolites); Sp–Py, *Climacograptus spiniferus*–*Geniculograptus pygmaeus* Zone boundary (graptolites). Note the relations between the base of the Cincinnatian in Ohio and the base of the Cobourgian in New York. Also, note the lower Cincinnatian facies changes along the cross-sections from the Trenton Shelf ramp to the Sebree Trough in southwestern Ohio and the Taconian Foreland Basin in New York and Quebec.

roundings were covered by calcareous shales and mudstones with subordinate interbedded limestones (Kope and Clays Ferry Formations). At the same time, carbonate deposition prevailed over most of the Trenton Shelf and formed a carbonate ramp with a gentle slope that extended southwestward toward the Cincinnati region. Toward the northeast and southeast, this ramp sloped into the Taconian Foreland Basin where increasingly coarse siliciclastics were deposited, apparently as a result of the formation of highland source areas to the east that were uplifted by Taconian orogenic movements.

4. Later, in the late *Geniculograptus pygmaeus* Chron, the fine siliciclastics of the Utica Shale spread westward from the foreland basin across the Trenton Shelf and portions of the Galena Platform. This dark shale deposition did not reach the Cincinnati region or other parts of the Lexington Platform, which remained sites of shallow-water carbonate and shale deposition. This was an apparent reversal of the depositional pattern established during early Cincinnati time, and it may have been related to local uplift of the Lexington Platform. During the remaining part of the Ordovician, thick, partly nonmarine siliciclastic sequences were deposited in New York and Quebec, whereas shallow marine sedimentation continued on the Lexington Platform through Richmondian time (Keith, 1989).

This report summarizes data, some of which are preliminary, from an ongoing regional study centered on the formation and development of the Sebree Trough. The emerging picture appears relatively consistent and simple, but much additional work is needed to fill in the many remaining blank areas.

Acknowledgments

We are most indebted to H. Hayes, K. Tyler, and B. Daye for invaluable technical assistance. R.J. Ross, Jr., and G.S. Nowlan reviewed the manuscript and provided constructive comments. The present research is a part of our studies on the evolution of the Sebree Trough, and grateful acknowledgment is made to the donors of The Petroleum Research Fund, administered by the American Chemical Society, for financial support supplied to SMB for this research. Partial page charges (\$1,000) obtained from the Petroleum Research Fund were applied to publication of this report.

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New hughmilleriid (Eurypterida) occurrence from the Tuscarora Formation, central Pennsylvania, and its environmental interpretation

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Abstract

A second eurypterid occurrence from the Tuscarora Formation of central Pennsylvania is reported. The eurypterid, a hughmilleriid, occurs in either a nonmarine or a brackish-estuarine environment. A highly resolved age cannot be determined for the occurrence, but it is probably Llandoveryan.

Introduction

In a *Festschrift* dedicated to Donald W. Fisher, former State Paleontologist of New York, it is appropriate to deal with a new Early Silurian hughmilleriid eurypterid locality. Dr. Fisher published a Silurian correlation chart for New York State in 1962, and was a key figure in the designation of a eurypterid as the official New York State Fossil. The eurypterid described in this report comes from nonmarine or possible brackish-estuarine beds in central Pennsylvania. Eurypterids of potential nonmarine origin are unknown elsewhere before the Wenlockian.

These remains are the second occurrence of megascopic eurypterid body fossils from the Tuscarora Formation in Pennsylvania. They are noteworthy because of their age and the scarcity of Early Silurian and older animal remains of unquestioned nonmarine origin (Gray, 1988). Nonmarine animal remains first began to be common in the Late Silurian.

The Tuscarora Formation, from which these fossils have been recovered, has long posed problems related to interpretation of the varied depositional environments that are apparently represented. One of Fisher's (1954) early papers dealt with similar interpretive problems posed by the varied depositional environments of the coeval Medina Group in western New York State and adjacent Ontario. A significant terrigenous influence was recognized in the Medina Group when land plant spores were found over 20 years ago (Gray and Boucot, 1971), and the lower Whirlpool Sandstone of the Medina Group has now been demonstrated to be nonmarine (Middleton et al., 1987; Rutka, written communication, 1988; Gray and Boucot, 1989).

The new fossil locality was found by D.M. Hoskins during an SEPM field trip in 1982. It was pointed out to Boucot because of Gray and Boucot's interest in finding Tuscarora nonmarine localities in which arthropod remains might be discovered. A.J. Boucot made the collection. J. Gray examined the material for organic-walled plant and animal remains of the type found elsewhere in the Tuscarora Formation (Gray,

1985), both to aid environmental interpretation and to obtain a more precise age reference for these otherwise unfossiliferous strata.

Earlier discoveries of Silurian eurypterids from Pennsylvania

Clarke and Ruedemann (1912, p. 418-420) briefly noted and listed eurypterids from the Tuscarora and Rose Hill Formations at Swatara Gap, Lebanon County, Pennsylvania. Similar eurypterids were reported and described by Clarke and Ruedemann (1912, pp. 417-418) from the Shawangunk Formation at the Delaware Water Gap, Pennsylvania, and from Otisville, New York, approximately 75 km to the northeast. The stratigraphic positions of fossils at all of Clarke and Ruedemann's localities were provided by Swartz and Swartz (1930, 1931). The age of the Shawangunk eurypterids within the Silurian is uncertain, although those at Otisville occur beneath strata with the fish *Vernonaspsis* (Denison, 1964) that are now assigned to the Late Silurian (Ludlovian, see below). The age of the Tuscarora eurypterids is discussed below.

A variety of arthropod-like, microscopic animal remains (Gray, 1985) are preserved in fluvial beds of the Tuscarora Formation at Millerstown, central Pennsylvania. These include some cuticle fragments with *Schuppen* and pores for sensory hairs that may be derived from eurypterids. Johnson (1985, p. 310-311) observed "megascopic coalified" animal remains in shales of the Tuscarora Formation that included "probable eurypterid parts" from an unspecified Tuscarora locality. Johnson did not state whether her locality represented fully marine, brackish, or nonmarine facies, although she implied that it was nonmarine.

New Silurian eurypterid locality

The new eurypterid locality is Stop 6 (a roadcut on the west side of Pennsylvania Highway 51 known as "Kishacoquillas Gap in Jack's Mountain") of the Guidebook for the SEPM Eastern Section's 1982 field trip (Cotter, 1982). The fossiliferous unit consists of a fine- to medium-grained, buff-weathering, rusty siltstone unit about 40 cm thick. The unit forms a weathered reentrant in the roadcut, within dominantly resistant quartzitic, unfossiliferous strata. The fossils, which occur as weathered casts and molds on siltstone slabs, were collected by splitting material from the fossiliferous bed. Other invertebrate fossils are unknown from the eurypterid-bearing unit.

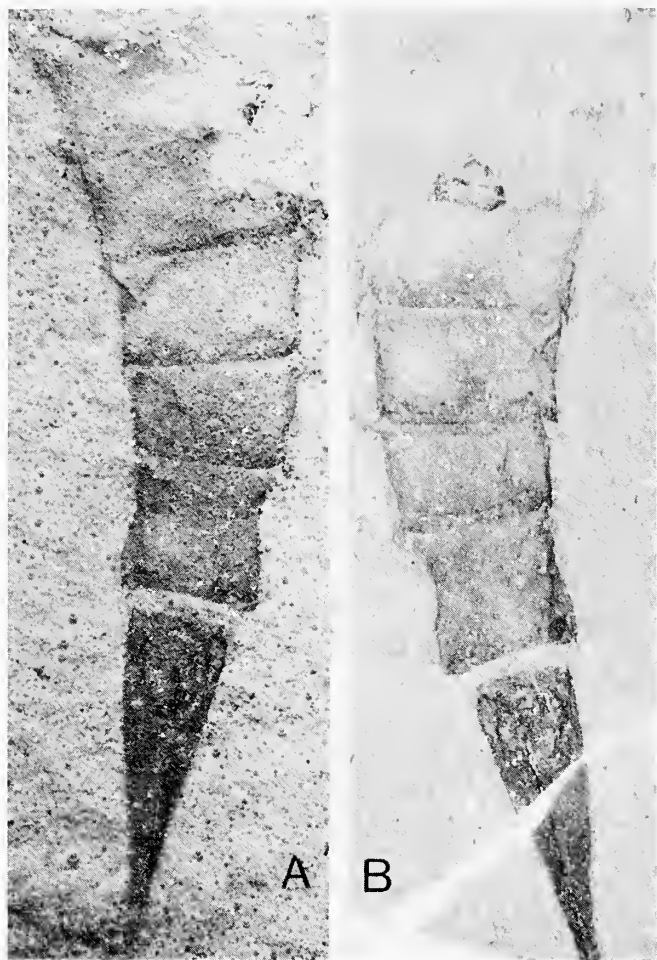


Figure 1. Hughmilleriid from the Tuscarora Formation, Pennsylvania. A, Internal impression (x3) of five post-abdominal segments of hughmilleriid eurypterid from Kishacoquillas Gap, north of Yeagertown, Pennsylvania. B, External impression (x3) of same specimen. Note absence of ornamentation. U.S.N.M. No. 451107.

Samples for palynological study were obtained from an olive drab siltstone interbedded with quartzites in the lower part of the Tuscarora Formation and from mudstone clasts in a quartzite unit from the underlying upper part of the Juniata Formation.

Typical Rose Hill Formation mudstones above the Tuscarora Formation in the roadcut yielded casts and molds of the brachiopod *Eocoelia*. The coarsely costate form and size indicate a pre-C₆ species that is older than *E. sulcata*.

Among the organic fragments, the only readily identifiable eurypterid remains consist of a cast and mold of a post-abdominal section with simple pointed telson, and five segments that are still articulated on the internal mold and four on the external mold (Figure 1). The manner of preservation, with the post-abdominal portion broken neatly from the abdominal segments, is common among all eurypterids (R. Plotnick, oral commun., 1989). The external surface is smooth and shows no evidence of striations, scales, or other ornamentation.

The specimen belongs to the Hughmilleriidae, as redefined by Stürmer (1973). Without some information about the head region and ventral characteristics, it is not possible to discriminate between *Hughmilleria*, *Nanahughmilleria*, and *Parahughmilleria*, and a generic assignment is not possible at this time. However, the post-abdominal segments and telson from Kishacoquillas Gap closely resemble *Hughmilleria*

shawangunk reported from both the Rose Hill and Tuscarora Formations at Swatara Gap and from the Shawangunk Formation.

Age

Fossils available in the Tuscarora Formation at the Kishacoquillas Gap section do not permit precise zonation of the eurypterid-bearing bed. The late Llandoveryan (pre-C₆) *Eocoelia* in the overlying Rose Hill mudstones provides an upper age limit for the Tuscarora in this roadcut. The presence of a hughmilleriid is inadequate evidence, by itself, for dating the locality. However, it is significant that all hughmilleriid localities from Otisville, New York to Swatara Gap near Lebanon, Pennsylvania, including the Delaware Water Gap area, are most easily interpreted from stratigraphic position and spore data to be of Llandoveryan age.

Berry and Boucot (1970) concluded that the Shawangunk Formation at Otisville, New York, lacked age-diagnostic fossils. However, all *Vernonaspis*-bearing beds detailed by Denison (1964), including those in the upper part of the Shawangunk Formation, are now assigned a Ludlovian age. The best dated *Vernonaspis* occurrence is on the south side of Baillie-Hamilton Island, Canadian Arctic, where the vertebrate-bearing beds are interbedded with strata containing Ludlovian graptolites (R. Thorsteinsson, oral commun., 1972). This information, plus the evidence summarized here, suggests that the lower part of the Shawangunk Formation with eurypterids is most likely of Llandoveryan age.

Samples processed for organic-walled microfossils from both the Tuscarora and the underlying Juniata Formations were barren of optically transparent material. However, spore tetrad-based dates indicate an age older than late Llandoveryan for the Tuscarora Formation at the Millerstown section approximately 20 km to the southeast (Gray, 1989).

Paleoenvironment

The depositional environment of the Tuscarora Formation ranges from fluvial in southeastern sections such as Millerstown, Pennsylvania, with land plant spores and arthropod-like remains (Gray, 1985), to interbedded fluvial/littoral-marine or fluvial/tidal-marine beds with *Skolithos* at Kishacoquillas Gap. *Arthropycus*-bearing beds, some associated with or interbedded with nearshore, more "normal" or open marine beds, occur to the northwest (Amsden, 1955).

It is uncertain whether the eurypterid-bearing bed described herein is freshwater or littoral-marine in origin. Its weathered condition precludes obtaining microfossil evidence, which is useful in demonstrating a nonmarine environment for the Tuscarora at Millerstown. However, the absence of *Arthropycus* at Kishacoquillas Gap, the absence of *Skolithos* near the eurypterid bed, and restriction of the eurypterid remains to a single horizon within the lowest exposed Tuscarora Formation are consistent with a nonmarine, if nearshore, depositional environment. In the section at Kishacoquillas Gap, Cotter (1982, p. 80, fig. 29, Bed 77) found rare *Skolithos* in braided fluvial deposits. He suggested that the presence of *Skolithos* indicates a "distal, near-coastal location" of these riverine deposits, which conforms to the general environmental interpretation for this biogenic structure elsewhere. Earlier studies by Smith (1970) and Smith and Saunders (1970) were concerned with the depositional environments of the Tuscarora Formation, and are in essential agreement with Cotter's conclusions and those of this report.

Gray (1988) has reviewed the evidence that suggests that the

Eurypterida were euryhaline. This interpretation further complicates the issue. However, most occurrences of *Hughmilleria*, *Parahughmilleria*, and *Nanahughmilleria* are from sites that can be interpreted as either freshwater or brackish-estuarine, as contrasted with an open or "normal" marine environment. The absence of normal marine invertebrate megafossils from the *Arthropycus*- and eurypterid-bearing parts of the Tuscarora Formation and its stratigraphic equivalents is a reason for concluding that these strata do not represent open marine environments, although, as noted above, *Arthropycus*- and *Skolithos*-bearing strata represent brackish-estuarine, marginal marine, or possibly tidal or littoral environments. In more normal marine beds of this age, abundant rhynchonellid brachiopods occur in nearshore environments (Boucot, 1975). Their absence in this section is consistent with other environmental information that suggests that the Kishacoquillas Gap hughmilleriid is among the oldest potentially nonmarine eurypterids.

Regional lithofacies relations

Amsden (1955) provided a useful lithofacies-biofacies analysis of Early Silurian strata of the central and eastern United States and adjacent Canada. His Figure 3 delineates an eastern lithofacies belt characterized by *Arthropycus*, which includes such units as the Medina Group of New York and adjacent Ontario and the Clinch and Tuscarora Formations of the central Appalachians. To the east of this linear siliciclastic belt with *Arthropycus*, Amsden (1955) outlined a still more easterly belt characterized by eurypterids, thereby implying that eurypterids and *Arthropycus* never occur together. Although they are associated in the Shawangunk Formation in the Otisville area, they do not co-occur in the typical eurypterid-bearing dark grey mudstones of the Shawangunk Formation (Swartz and Swartz, 1931).

Amsden (1955) recognized this eurypterid-bearing lithofacies-biofacies unit only in the Otisville, New York, area through the Delaware Water Gap region in New Jersey and adjacent Pennsylvania. Available information based on the new eurypterid locality at Kishacoquillas Gap and data from Swatara Gap and Millerstown, Pennsylvania, suggests that it is reasonable to extend Amsden's eurypterid-bearing facies belt southwest to the Susquehanna River region. Amsden (1955) was concerned about the lack of age-diagnostic fossils from Otisville, New York, to Swatara Gap, Pennsylvania, but more recent work on the higher land plant spore tetrads (Gray, 1989) makes it clear that the Tuscarora Formation at Millerstown, Pennsylvania, is pre-late Llandoveryan in age.

Acknowledgments

We are indebted to R. Plotnick, University of Illinois at Chicago, for advice about the identity of the eurypterid and for critically examining the manuscript, and to I. Rolfe, National Museum of Scotland, Edinburgh, for reviewing the manuscript. We thank Alfred Potter, Oregon State University, for providing the photographs.

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Paleoautecology and ontogeny of *Cupulocrinus levorsoni* Kolata, a Middle Ordovician crinoid from the Guttenberg Formation of Wisconsin

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Abstract

Cupulocrinus levorsoni Kolata is a cladid inadunate crinoid from the Middle Ordovician Guttenberg Formation of southwestern Wisconsin. These cupulocrinids are associated with the large camerate crinoid *Pycnocrinus gerki* Kolata. The crinoids inhabited a well-circulated area with a substrate consisting of carbonate mud and strophomenid brachiopod shells. The crinoid community was buried in place by fine-grained sediment and the remains of a "bloom" of floating cyanobacteria or eukaryotic algae.

A growth sequence of complete crowns preserving the food grooves and covering plates is available for *Cupulocrinus levorsoni*. Analogies with Recent crinoids permit reconstruction of its feeding habits and food-gathering capacity. *Cupulocrinus levorsoni* attached to objects on or above the seafloor with a stem coil at the end of its comparatively short column. The animal was a passive suspension feeder and probably held a roughly planar or parabolic arm fan that was oriented in a radial posture.

New arm branches developed throughout the ontogeny of *Cupulocrinus levorsoni*. Consequently, the size of the food-gathering system, as given by its length, number of brachial plates, and number of food-catching tube-feet, exhibits marked positive allometry relative to crown volume. Thus the food-gathering system grows more rapidly than would be the case for isometry. Food-gathering capacity is estimated by the number of food-catching tube-feet multiplied by the width of the food grooves. Food-gathering capacity is positively allometric compared to the isometric exponent. The ratio of food-gathering capacity/crown volume declines slowly during ontogeny.

The spacing of the food-catching tube-feet of *Cupulocrinus levorsoni* is constant regardless of size, and is similar to that of modern crinoids. Branch density (number of arm branches divided by area spanned by the arms) decreases in larger crinoids, so that the branches of adults are relatively more dispersed than in young individuals. Slightly wider food grooves are observed in larger individuals.

Comparison of the food-gathering parameters of *Cupulocrinus levorsoni* and *Pycnocrinus gerki* reveals similarities and differences. The columns of the pycnocrinid are typically longer than those of the cupulocrinid; this implies that the two species fed at different levels. Both forms probably ate similar-sized food as indicated by the width of the food grooves. *Pycnocrinus gerki* is characterized by larger tube-foot spacings and higher branch densities than *C. levorsoni*. This contrast may be attributed to different current velocities at the elevations and/or feeding intervals utilized by the two species, or to alternative feeding

patterns. It is possible that the pycnocrinids trapped food mainly by inertial impact and direct interception, whereas the cupulocrinids were specialized for motile particle collection and gravitational deposition.

Introduction

Years ago, Donald Fisher suggested that one of us, JCB, study the functional morphology, growth, and variation in *Lasiocrinus scoparius* (Hall) from the Lower Devonian Coeymans and Manlius Limestones of New York. Unfortunately, this project was never completed, but this report is tendered as a substitute. The purpose is to describe the paleoautecology of *Cupulocrinus levorsoni* Kolata (1986), a Middle Ordovician crinoid belonging to the cladid inadunates from the northern Midcontinent. This report emphasizes two aspects of the species' paleoautecology. The first is the ontogenetic development of the capacity of the food-gathering system. Second, inferences will be made about its feeding behavior and the dimensions of its ecological niche.

All specimens were obtained from a single horizon 3 m above the base of the Glenhaven Member of the Guttenberg Formation (Galena Group; Middle Ordovician, Rocklandian Stage; see Kolata, 1986; Willman and Kolata, 1978; Templeton and Willman, 1963 for discussion of lithologies and faunas). Two localities are involved: (1) Quarry on north side of State Rte. 35, 4 km northeast of Beetown, Grant County, Wisconsin (SE1/4, NE1/4, NW1/4, sec. 16, T4N, R4W, Hurricane 7 1/2-minute Quadrangle); (2) Quarry 6 km south of Annaton, Grant County, Wisconsin (SE1/4, SW1/4, SE1/4, sec. 25, T5N, R2W, Ellenboro 7 1/2-minute Quadrangle). The lithology consists of yellow or brown lime mudstone in wavy beds 4.0 to 10.0 cm thick; the limestone beds are separated by thinner brownish shaly partings. Crinoids are found on the upper bedding planes of the limestone and in the shaly partings. The associated fauna includes numerous specimens of *Pycnocrinus gerki* Kolata (1986), a large glyptocrinid camerate crinoid, and strophomenid brachiopods belonging to the genus *Rafinesquina*; smaller numbers of other strophomenid and orthid brachiopods, fragments of isotelid and other trilobites, upright ramose and bifoliate bryozoans, encrusting bryozoans, holdfasts of unknown echinoderms, and a starfish are also present (Table 1). The crinoids are highly concentrated and occur on bedding planes ranging from 0.25 to 1.0 m² in area.

Based on a regional survey of the Middle Ordovician of the northern Midcontinent, Sloan (1987) concluded that the Guttenberg Formation was deposited on a equatorial shelf at depths of approximately 10 to 20

Table 1. Faunal composition of crinoid assemblage.

Species	Number of Specimens	Percent
Echinoderms		
<i>Cupulocrinus levorsoni</i>	55	21.6
<i>Pycnocrinus gerki</i>	31	12.2
Undetermined star-shaped holdfasts on <i>Rafinesquina</i>	2	0.78
Undetermined starfish	1	0.39
Undetermined cystoid	1	0.39
Brachiopods		
<i>Rafinesquina</i> sp.	98	38.4
<i>Strophomena</i> sp.	15	5.88
<i>Dinorthis</i> sp.	11	4.31
<i>Hesperorthis tricenaria</i>	5	1.96
<i>Sowerbyella</i> sp.	5	1.96
Trilobites		
Unidentified phacopid	14	5.49
Unidentified isotelid	5	1.96
Undetermined ceraurid	1	0.39
Bryozoans		
Ramose fragments	5	1.96
Bifoliate fragments	5	1.96
Encrusting colony on <i>Rafinesquina</i>	1	0.39
Totals	255	100.0

Table 1. Faunal composition of crinoid-bearing assemblages.

m. The overall lithology indicates that the animals lived on fine and soft muds with adequate circulation of the surrounding seawater (e.g., Sloan, 1987; Kolata and Jollie, 1982; Willman and Kolata, 1978). The fact that the fauna is dominated by filter- and suspension-feeders also denotes well-circulated conditions. Beds of shell hash and fossil debris can be attributed to storm deposits and/or bioturbation.

Kolata and Jollie (1982) originally interpreted the shaly partings as inflows of argillaceous and carbonate mud that were produced by storms. However, recent work by Jacobson et al. (1988) revealed a different origin (D.R. Kolata, personal commun., 1990). In the subsurface, the shaly partings contain from 8.2 to 43.3% of organic carbon by weight. The dominant organic component is composed of *Gloeocapsamorphia prisca*, a colonial microfossil of uncertain systematic affinities (Assemblage A of Jacobson et al., 1988). Possible assignments of this species are to the blue-green algae (cyanobacteria) or eukaryotic algae (Burns, 1982; Hoffmann et al., 1987; Reed et al., 1986). *Gloeocapsamorphia* may have been chemo- or phototropic (compare Hoffmann et al., 1987 and Reed et al., 1986). Most workers agree on a planktic lifestyle. It is possible that the benthic macrobiotic communities were buried in place by the dead and dying remains of a "bloom" of microorganisms along with an influx of clastic and carbonate sediment.

Aside from breakage of the stems, the echinoderms are essentially intact, and this condition testifies to rapid burial. Recent echinoderms, such as crinoids and ophiuroids, fragment rapidly and will be reduced to isolated plates in several (two to six) days by the action of waves,

currents, scavengers, and the usual agents of decomposition (Lewis, 1980). The echinoderms on the limestone beds overlie the brachiopods, bryozoans, and trilobites. Many of the latter fossils were disarticulated, sometimes broken, and perhaps moved before burial of the crinoids. Most strophomenid valves are found in a hydrodynamically stable position with the convex side up; this is the reverse of the most likely living position. In addition, a few of the convex-upward strophomenid shells lay on the seafloor long enough to be colonized by encrusting bryozoans and the digitate holdfasts of *Pycnocrinus gerki*. Obviously, the crinoids populated a substrate that was largely covered by live and dead shells of brachiopods and other organisms. After the crinoid colony became established on this surface, it persisted for some time, only to be overwhelmed and buried by a flood of *Gloeocapsamorphia prisca* and associated sediment.

Morphology of *Cupulocrinus levorsoni*

This species (Plates 1-4; Figure 1) is a rather unusual member of the genus, and it is necessary to discuss its taxonomic affinities in some detail. The aboral cup is steeply conical, the arms branch isotomously, and a long and slender anal tube is present (see Kolata, 1986, for description). Compared to most cupulocrinids, the cup of *Cupulocrinus levorsoni* is relatively small, and the arms are long and slender with numerous branches. This feature of this Guttenberg crinoid species resembles dendrocrinids more than typical cupulocrinids. The radial facets occupy 72% of the width of the radial plates. This figure is less than that of most cupulocrinids, which bear wider radial facets (Brower, In press). Species currently placed in *Dendrocrinus* have variable radial facets, but most are more narrow than in *C. levorsoni*.

The anal tube of the Guttenberg animal is much more similar to that of cupulocrinids than that of dendrocrinids. The adanal side of the anal tube consists of a single row of large hexagonal plates; the median row is flanked by several rows of slightly smaller and less regular plates. The abanal part of the anal tube is made up of small irregular plates (see Plate 1, figure C; Plate 2, figures C, E; Plate 3, figures C, E, for anal tube morphology). The anal tube of dendrocrinids has rows of regular, typically hexagonal, and equal-sized plates that are commonly plicate.

Unfortunately, the articular surfaces of the radial facets and the brachials are poorly preserved in *Cupulocrinus levorsoni*, and their exact nature cannot be determined. Some adult specimens exhibit small gaping lips on the aboral sutures of the primibrachs and secundibrachs (Kolata, 1986, p. 712). This type of structure suggests the presence of "petaloid processes" as known in *Cupulocrinus* and flexible crinoids (e.g., Springer, 1911).

These features of the calyx indicate that *Cupulocrinus levorsoni* has more affinities with cupulocrinids than with dendrocrinids, and the species should be assigned to *Cupulocrinus* as proposed by Kolata. The overall dendrocrinid aspects of the arms in *C. levorsoni* could represent shared similarities with dendrocrinids, or convergent evolution. These two possibilities cannot be differentiated without a detailed phylogenetic analysis.

One young specimen (near paratype IGS 79P-27; Plate 4, figure B; Figure 1G) has a complete anal tube with the anal opening at its distal end. This is of interest because this structure is rarely preserved in cladid inadunate crinoids.

Food grooves and covering plates are so well preserved in the Guttenberg specimens that the entire food-gathering system can be reconstructed (e.g., Plate 1, figure B; Plate 3, figure E; Figures 1A-



A

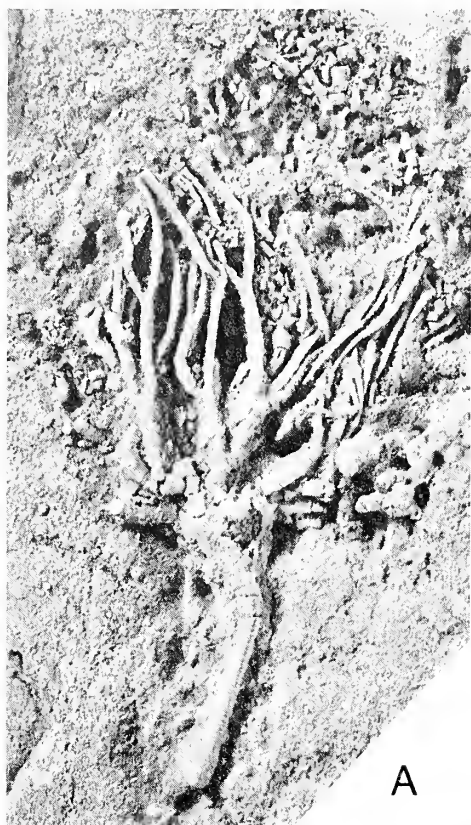


B



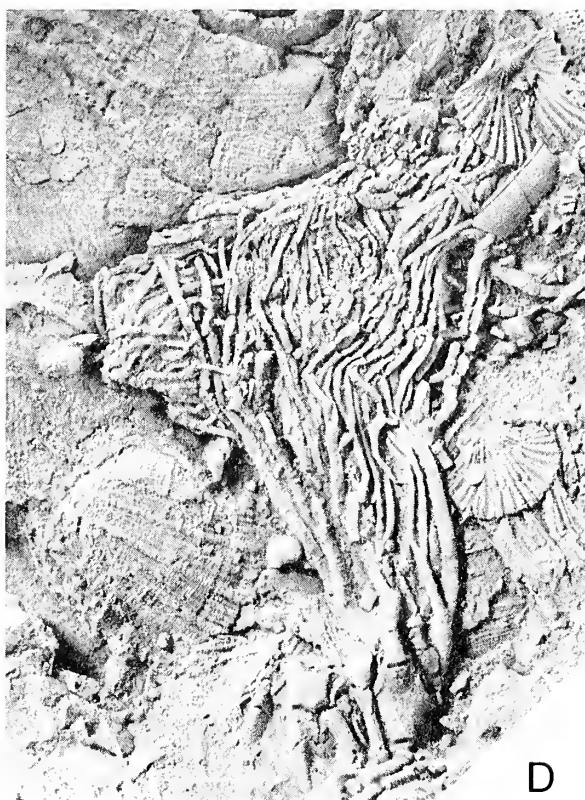
C

Plate 1. Adults of *Cupulocrinus levorsoni* Kolata. A, Crown showing long and slender arms, paratype SUI 50868, x2.5. B, Flattened arms preserving food grooves and covering plates on many brachials. Arms seem to be preserved in a planar filtration fan. Note lack of gaps and deformation of arms, paratype SUI 50875, x4. C, Crown with anal tube showing abanal side with irregular plates. Observe bends denoting flexibility of distal arms, holotype SUI 50872, x2.5.

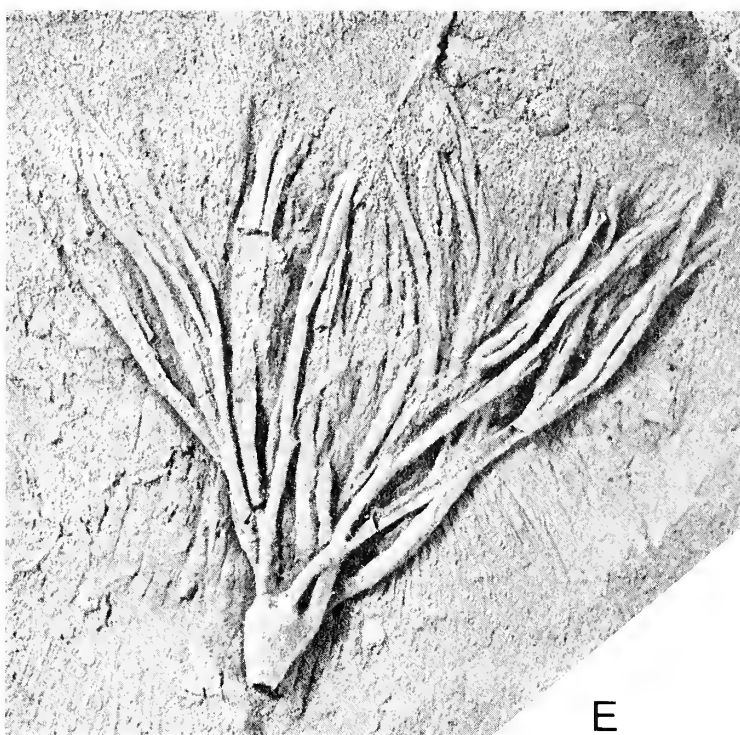


B

C



D



E

Plate 2. Young specimens of *Cupulocrinus levorsoni* Kolata. Paratypes, x4. A, Crown with tangled arms and column segment, IGS 79P-34. B, Incomplete specimen with well-preserved aboral cup, IGS 79P-3. C, Somewhat disarticulated individual showing plate arrangement for lateral side of anal tube. Note row of large plates flanked by smaller and less regular plates, IGS 79P-5. D, Complete crown associated with brachiopods. Some covering plates and food grooves are present. Bends in arms suggest flexibility, IGS 79P-6. E, Specimen displaying arm branching pattern and excellent aboral cup. Adanal side of anal tube shows large and regular plates, IGS 79P-2.



A



B



C



D



E

Plate 3. *Cupulocrinus levorsoni* Kolata. A, Small specimen with well-preserved cup and long column segment. Small arm in center is suggestive of regeneration, paratype IGS 79P-26, x4. B, Mid-sized crinoid with well-preserved cup and part of one ray, paratype IGS 79P-20, x4. C, Small slab with well-preserved individual in mid-sized range. Note long column segment, complete arm, and part of adanal side of anal tube with large and regular plates, paratype SUI 50870, x3. D, Column segments of small crinoids with distal coils. Specimen on right bears a rounded termination, left coil ends in a normal columnal. Figured specimens located near paratype IGS 79P-22, x4. E, Crushed adult with food grooves and many covering plates. Proximal portion of adanal side of anal tube has large and regular plates, paratype IGS 79P-41, x3.



A



B



C



D

Plate 4. Juvenile specimens of *Cupulocrinus levorsoni* Kolata. *A*, Smallest known crown, although not well preserved, the aboral cup, abanal side of anal tube, food grooves and covering plates are clearly present. Figured specimen near paratype IGS 79P-27, x8. *B*, Fragment of distal part of anal tube; note small and irregular plates with anal opening at tip. Figured specimen near paratype IGS 79P-27, x6. *C*, Slightly disarticulated and partial crown, paratype IGS 79P-31, x7. *D*, Complete crown with long column segment and splayed arms associated with stems of other crinoids, paratype IGS 79P-22, x4.

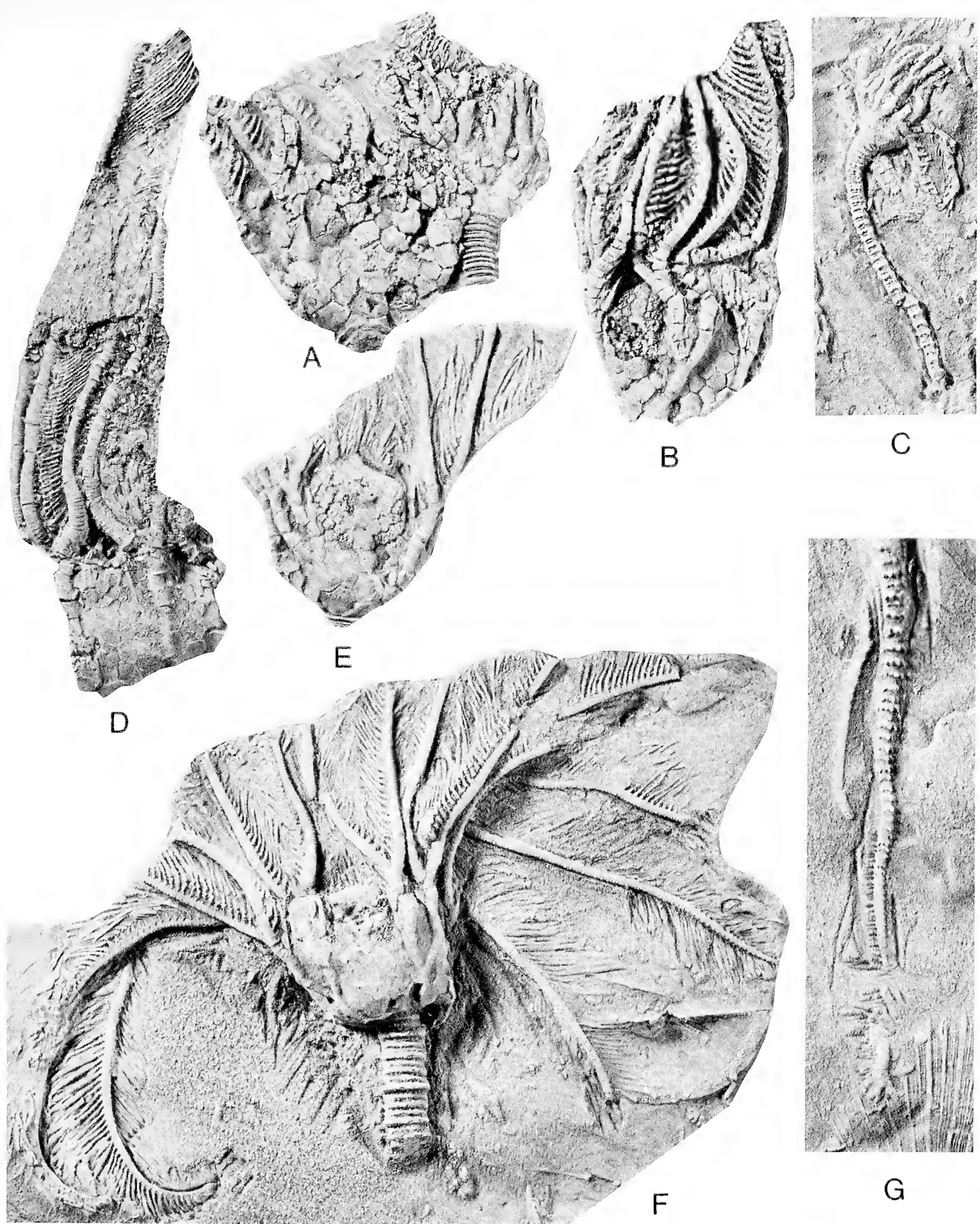


Plate 5. *Pyncocrinus gerki* Kolata. Four pinnulate arms are present in each ray, and adults possess numerous brachials that are fixed or incorporated into the aboral cup. *A*, Mature and immature calyces, paratypes SUI 50860 (left) and 50861 (right), x3. *B*, Well-preserved aboral cup with proximal parts of arms, pinnules clearly shown, paratype IGS 79P-13, x3. *C*, Young crinoid with relatively few fixed brachials in cup, short arms, and long column segment, paratype IGS 79P-1, x2.5. *D*, Largest known individual, a partial cup illustrating some arms and pinnules, paratype IGS 79P-40, x2. *E*, Partial crown with posterior interrays, tegmen, proximal arms, and pinnules, holotype, SUI 50871, x3. *F*, Large crown with portion of column and complete arms with long and slender pinnules, paratype SUI 50852, x2. *G*, Column with digitate holdfast attached to a strophomenid brachiopod shell. A poorly preserved crown is present but not shown on the photograph, paratype SUI 50846, x3.

E). The observed bends of the columns indicate that they were at least moderately flexible (Plate 3, figure D; Plate 4, figure D). The method of attachment is uncertain because complete stems have not been seen attached to crowns. Several column segments closely associated with crowns of *Cupulocrinus levorsoni* have a coiled distal tip (Plate 3, figure D; Figure 1F). The known coils are not wrapped around solid objects. The end of at least one specimen tapers bluntly and must have been terminal. This suggests that the species was attached by a column coiled on the substrate or around some soft object on or above the seabed. The distal columnals have sharp margins, which probably helped the animal to attach and adhere. Stems of this type are known in species assigned to various crinoid genera such as *Pycnocrinus*, *Alisocrinus*, and *Ctenocrinus* (e.g., Ehrenberg, 1929; Brett, 1981).

Size frequency distribution and mortality rates

A growth sequence of *Cupulocrinus levorsoni* is based on thirty-five specimens that range from 1.75 to 4.65 mm in cup height (Plates 1-4; Figure 1). The frequency distribution shows that young specimens are most common (Figure 2A). The smallest and youngest animals are well beyond the larval stages, and the arms are well-developed with eight isotomous branches per ray. Adults bear much longer arms, with up to forty isotomous branches in a ray. The survivorship curve is convex upward (Figure 2B). Cup height is shown on a logarithmic scale because linear measures of size are commonly logarithmically distributed with respect to the individuals' ages (Dodd and Stanton, 1981). The graph indicates a gradually increasing mortality until a cup height of about 4.0 mm was attained. The few available data imply that larger crinoids were subject to lower mortality rates. Similar patterns are

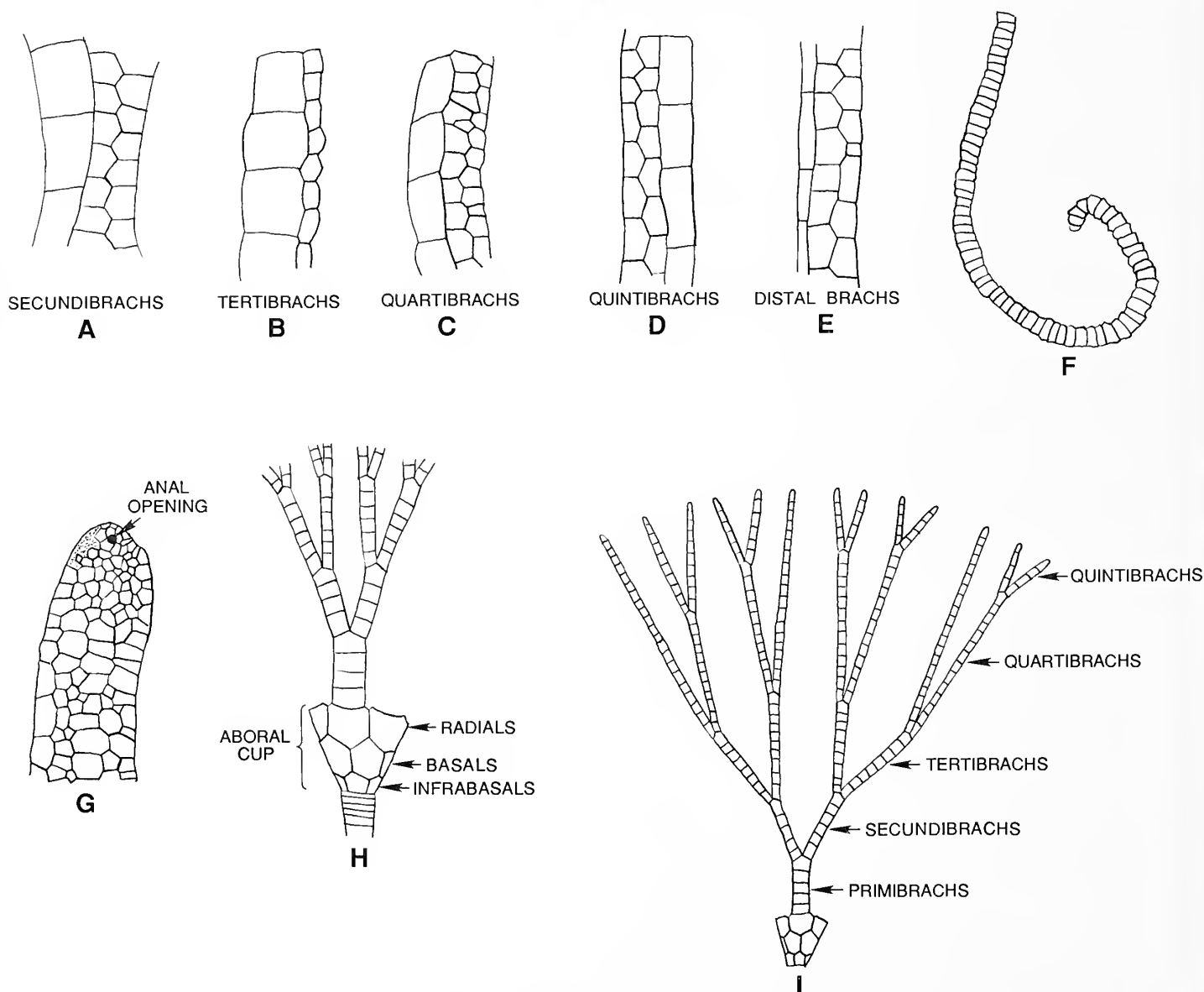


Figure 1. Diagrams showing morphology of *Cupulocrinus levorsoni* Kolata. A-E, Arm segments showing brachials with covering plates for adult crinoid. Brachials from left to right are secundibrachs, tertibrachs, quartibrachs, quintibrachs, and hexibrachs or septibrachs, paratype SUI 50875, A-C x16, D-E x32. F, Coiled stem segment of young animal, figured specimen near IGS 79P-22, x7.8. G, Distal part of anal tube of juvenile. Stippling denotes area where plate structure cannot be ascertained, figured specimen near IGS 79P-27, x16. H, Aboral cup and proximal arms of adult, modified from paratype SUI 50868, x3.9. I, Aboral cup of immature crown with one ray restored in food-gathering orientation, based on paratype IGS 79P-2, x3.9.

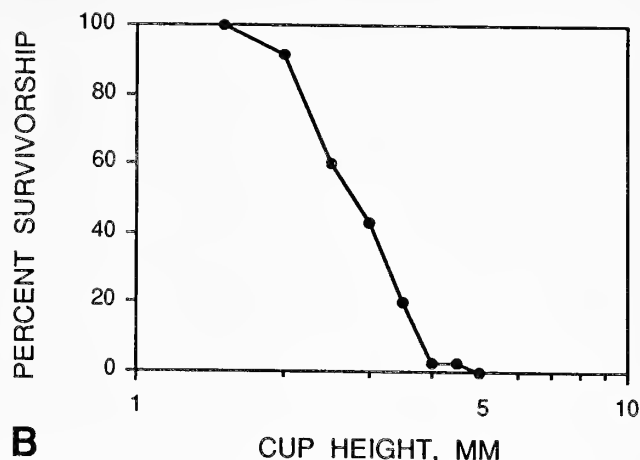
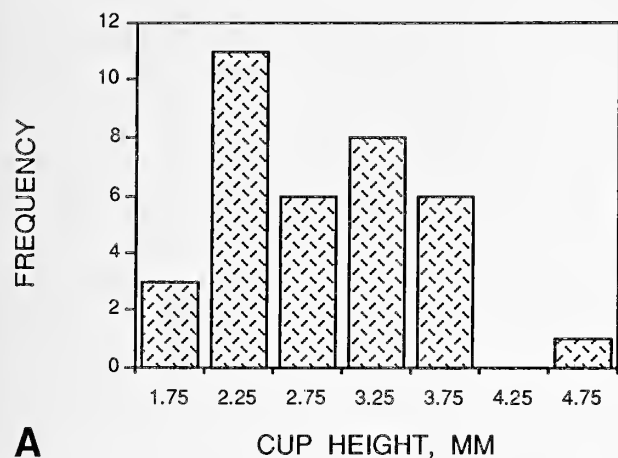


Figure 2. Size-frequency distribution and survivorship graphs for *Cupulocrinus levorsoni* Kolata. A, Histogram for cup height. B, Survivorship graph.

known in various Ordovician camerate crinoids (Brower, 1973), other cupulocrinids (Brower, in prep.), and other Paleozoic invertebrates (see Dodd and Stanton, 1981, for review).

Food-gathering in modern crinoids

Feeding in living crinoids has been reviewed by Meyer (1982a) and Lawrence (1987). All extant crinoids are passive suspension feeders (see Rubenstein and Kuehl, 1977). Two feeding postures have been observed. At times of slack water, some crinoids from deep water spread their arms horizontally. Food particles that fall vertically are caught by the tube-feet. However, most Recent crinoids from deep and shallow water are at least moderately rheophilic and live in areas with currents. The arms form several types of planar, parabolic, or conical filtration nets that are oriented approximately at right angles to the current. The food grooves and tube-feet face down-current; food particles carried by the current impinge on or are caught by the tube-feet.

The discussion of the depositional setting presented above indicates

that the environment was well-circulated. Consequently, these Ordovician crinoids were mainly rheophiles. A schematic restoration of a young individual engaged in feeding is given in Figure 3. The orientation is loosely based on the radial posture of Recent stalked crinoids (Macurda and Meyer, 1974) and comatulids in which columns are lacking in adults (Meyer, 1982a; Lawrence, 1987). Note that fecal material emerging from the anus at the distal end of the anal tube would be carried down-current and well away from the arms. Thus there was no danger of the food-gathering system being fouled with feces. When the animal was not feeding, the arms were probably held approximately vertically, as observed in living animals. Once in the proper orientation, the ligaments of the column and arms were presumably locked in place to hold the stem and crown in position with little expenditure of effort, as can be done by many living echinoderms (e.g., Motokawa, 1985). The variable orientations of the arms observed in specimens (e.g., SUI 50875) demonstrate that the distal parts of the arms were at least moderately flexible. If an individual of *Cupulocrinus levorsoni* became detached, either accidentally or voluntarily, it may have been able to crawl with the arms and eventually

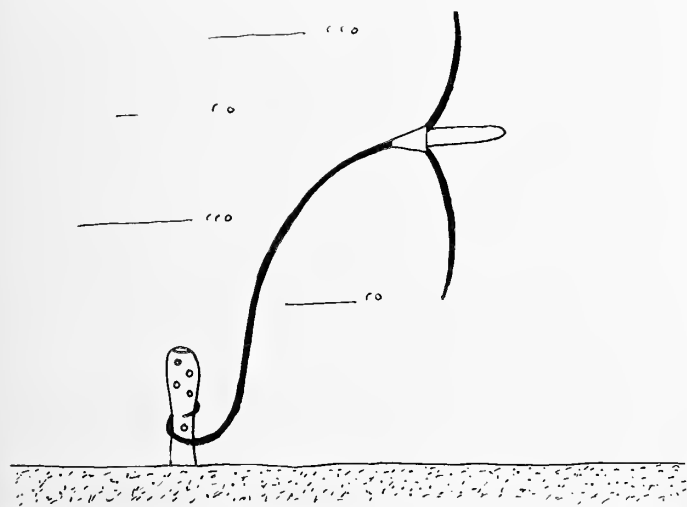


Figure 3. Schematic restoration showing *Cupulocrinus levorsoni* Kolata in food-gathering position. Based on small specimens and column segments near paratypes IGS 79P-22 and 27, the sponge is hypothetical, approximately x3.

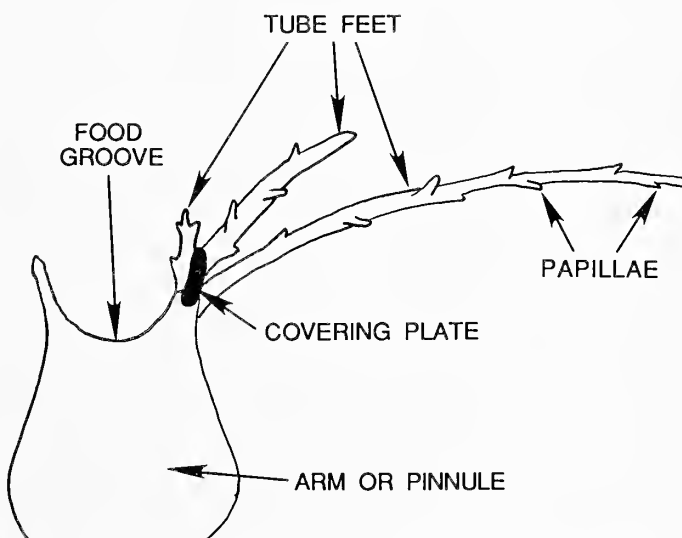


Figure 4. Sketch of modern crinoid arm illustrating food groove and tube feet. Redrawn from Meyer (1982a, fig. 2B), approximately x150.

relocate elsewhere, as observed by Messing et al. (1988) for a modern stalked crinoid.

The food-catching mechanism of modern stalked and comatulid crinoids is well-known (Lawrence, 1987; Meyer, 1982a; Nichols, 1960). The tube-feet are grouped in triads, each of which is linked to a lappet or covering plate (Figure 4). Each set of tube-feet contains one long, one short, and one intermediate length tube-foot. The tube-feet are papillose and covered with mucus. Most food particles are caught by the primary or long tube-feet, but some are taken by the secondary tube-feet. Food particles are moved to the food grooves by wiping of the tube-feet in the food grooves, or they are transferred by the shorter tube-feet. Once in the food grooves, the food is wrapped in mucus and carried to the mouth by ciliary transport. Occam's razor will be applied herein, and it will be assumed that this arrangement was present in fossil crinoids; certainly, there is no evidence to the contrary. If so, one can determine the number of tube-feet by counting the number of covering plates. When the animal is not feeding, the tube-feet are retracted and the covering plates close and roof over the food grooves.

Many variables affect the feeding of modern crinoids. Some are related to behavior patterns — for example, the length of the feeding intervals and the proportion of the available food in the water that is actually caught and eaten. The food content of the seawater, exact current velocities, and similar environmental characters are also critical. Obviously, such parameters must remain largely unknown for fossils. Nevertheless, some pertinent features can be estimated or inferred from the skeleton. Within recent years, crinoid specialists have tabulated four such variables (e.g., Ausich, 1980; Meyer, 1982a). The first two characteristics are related to the dimensions of the niche, whereas the latter two are correlated with feeding mode.

1. Elevation above the substrate probably defines the primary niche dimension (Ausich, 1980; see Bottjer and Ausich, 1986, for history of tiering during the Phanerozoic). Unfortunately, data on stem length in crinoids are rare and equivocal. *Cupulocrinus levorsoni* was attached to the substrate or to some elevated object by a distal stem coil. A detached coiled stem near several young specimens (Plate 3, figure D; Figure 1F) is thought to be complete because its proximal plates resemble those of the associated crowns. This stem indicates an elevation of approximately 20 mm above the host object for the smaller crinoids (cup height 1.75 to 2.5 mm). Incomplete columns up to 50 mm long have been observed joined to crowns with cup heights of 3.5 to 4.0 mm. If *C. levorsoni* was attached to the sea floor, it occupied a lower level or tier than *P. gerki*.

Pycnocrinus gerki possessed a much longer stalk (Plate 5). A juvenile (cup height about 5.0 mm) bears an entire stem, 40 mm long, with a digitate holdfast attached to a strophomenid shell (Plate 5, figure G). The cup of adult specimens of *P. gerki* is roughly 20 mm high (Plate 5, figures D, F). Broken column segments vary from 30 to 45 cm long and obviously belong to mature pycnocrinids.

Both *Pycnocrinus gerki* and *Cupulocrinus levorsoni* must have lived well above the brachiopods and trilobites and perhaps the bryozoans. This conclusion is based on the sizes of the fragments of the bryozoan colonies that have been collected.

2. Most food particles (over 90%) processed by modern crinoids are smaller than the food groove width (Rutman and Fishelson, 1969; Fishelson, 1974; Meyer, 1982a, 1982b), and it seems reasonable to adopt the food groove width as an approximate upper limit on food particle size. Ausich (1980) inferred that food size represents a second-order niche parameter, and different species that coexisted at the same level probably ate food of different sizes.

3. The tube-foot-spacing, or the number of primary or food-catching tube-feet per mm along one side of an arm or pinnule, is related to the environment and the feeding technique (Meyer, 1979, 1982a; Kammer, 1985). This parameter must reflect small-scale patterns of water flow in the immediate vicinity of the tube-feet. Meyer (1979, 1982a) reported that the tube-foot spacings of twenty-two species of Recent crinoids vary from 4.59 to 9.49 tube-feet per mm. Closely spaced tube-feet tend to be short. These species dwell in agitated locales dominated by currents that are unidirectional at any one time, and Meyer suggested that the food is mostly gathered by direct interception and inertial impact. Longer tube-feet are typically more widely spaced. Crinoids with longer tube-feet live in habitats with slower and more varied current directions; the common feeding mechanisms are attributed to motile particle collection and possibly to gravitational deposition.

4. The branch density consists of the number of arm branches in all rays divided by the area spanned by the arms during feeding (Ausich, 1980). The calculated area is based on a round and flat food-gathering net. Several individuals of *Cupulocrinus levorsoni* are preserved with the arms spread in this orientation. The arm segments show no evidence of separation or distortion. This fact demonstrates that the animal could have maintained a planar arm fan or perhaps a parabolic arm net. Of course, similar areas would be spanned by parabolic and planar arm patterns. Branch density illustrates the large-scale pattern of arm branching. Branch density and food groove width are negatively correlated in many crinoids (Ausich, 1980).

Statistical techniques

Allometry is defined by shape changes that are linked with size increase or decrease. The developmental patterns of *Cupulocrinus levorsoni* are bivariate and can be described with the allometric equation or simple power function (see Gould, 1966, 1971, 1977, for reviews; Brower, 1987, for application to crinoids). The equation is $Y = aX^b$. Y and X are variables. The initial intercept a gives Y when X equals 1.0, and the exponent b represents the ratio of the specific growth rates of Y and X . The exponent also dictates the behavior of Y/X . If the exponent

Y Axis	X Axis	Exponent
Linear dimension	Linear dimension	1/1 or 1.0
Area	Area	2/2 or 1.0
Volume or mass	Volume or mass	3/3 or 1.0
Area	Linear dimension	2/1 or 2.0
Volume or mass	Linear dimension	3/1 or 3.0
Linear dimension	Area	1/2 or 0.5
Linear dimension	Volume or mass	1/3 or 0.33
Area	Volume or mass	2/3 or 0.67
Volume or mass	Area	3/2 or 1.5

Table 2. List of isometric exponents for various dimensions.

Equation No.	X Variable	Y Variable	Exponent	Initial Intercept	Initial Intercept (logarithms)	Correlation Coefficient	Standard Error of Intercept (logarithms)	Standard Error of Exponent	Isometric Exponent	Student's <i>t</i>	No. of Specimens	Minimum X	Minimum Predicted Y	Maximum X	Maximum Predicted Y
1	Cup height	Distal cup width	1.23	0.924	-0.0345	0.929	0.0456	0.0999	1.0	2.33*	21	1.75	1.84	4.65	6.14
2	Cup height	Stem facet width	1.05	0.301	-0.521	0.840	0.519	0.116	1.0	0.400	24	1.75	0.541	4.65	1.50
3	Infra-basal height	Infra-basal width	1.09	0.877	-0.0571	0.804	0.0183	0.138	1.0	0.639	22	0.55	0.457	1.20	1.07
4	Basal height	Basal width	1.10	0.787	-0.104	0.882	0.0192	0.119	1.0	0.824	19	0.90	0.701	1.90	1.59
5	Radial height	Radial width	1.32	1.110	0.0469	0.907	0.0121	0.122	1.0	2.66*	21	0.85	0.898	1.50	1.91
6	Radial width	Radial facet width	1.10	0.697	-0.157	0.859	0.0270	0.150	1.0	0.644	14	1.00	0.697	2.10	1.57

Table 3. Equations for growth of aboral cup in *Cupulocrinus levorsoni*. Student's *t*-test values that are significant at the 0.05 level are indicated by asterisk (*).

is zero, then Y remains the same regardless of X. With a negative exponent, Y decreases as X increases. Given a positive exponent, Y increases as X increases. Where *b* equals 1.0, then Y/X and the growth rate of Y per unit increment of X are stabilized. If the exponent is greater than 1.0, Y grows more rapidly than X, and Y/X becomes larger with larger values of X. With *b* less than 1.0, then Y grows less rapidly than X and Y/X declines with larger X.

The shape of an isometric organism is the same at all sizes. Isometry or geometrical similarity represents a useful comparison with respect to the observed data. If isometry is applicable, then areas must be functions of squared linear dimensions, whereas volumes, masses, and weights would be proportional to cubed linear dimensions. Isometric exponents are listed in Table 2. Student's *t*-tests are used for comparing the observed and isometric exponents. If the observed exponent significantly exceeds the isometric one, the organism shows positive allometry for shape, and Y grows more rapidly relative to X than would be the case for an isometric animal. Negative allometry is present if the observed exponent is smaller than the isometric one. All equations are computed with the reduced major axis algorithm (Imbrie, 1956).

Mann-Whitney U tests are used for comparison of the food-gathering parameters of *Cupulocrinus levorsoni* and *Pycnocrinus gerki* instead of a Student's *t*-test. This technique was applied because of the small size and somewhat erratic distributions of the samples (Siegel, 1956).

Measurements

Most parameters in paleontological and biological studies are indirectly related to the functions that they are supposed to represent (see Gould, 1966, for review). A common example is the use of a linear dimension as a surrogate for size. Obviously, this procedure can be

valid only if the linear dimension is isometric with respect to a more legitimate size variable such as body volume or mass. The point is critical, and the measurements selected here are designed to replicate the original functional relationships as closely as possible, in addition to portraying the geometry of growth. All linear units are in millimeters. A list of the measured characters includes the following:

- A. Aboral cup variables (Table 3): (1) Height of dorsal cup from stem facet to distal margin of radials. The cup height gives a convenient linear measure of size and relative age for the geometrical aspects of ontogeny. (2) Cup width at level of radial facets. (3) Heights and widths of cup plates. (4) Width of stem and radial facets.
- B. Brachial parameters (Table 4): (1) Height. (2) Width. (3) Width of food groove. (4) Height of one covering plate as measured parallel to the long axis of the arm.
- C. Overall size variables (Table 5): The height of the aboral cup does not yield an acceptable measure of size for dealing with food-gathering. In this case, size would be the volume or mass of tissue that must be supplied with food. Unfortunately, this character cannot be measured for fossils. However, the crown volume can be computed, although this feature does not include the stem. Judging from the few specimens that are nearly complete, the crown volume is much less than that of the crown. Ignoring the stem is also consistent with the fact that it contained little soft tissue. Treating crown volume as a surrogate for size and relative age assumes that the volume and mass of soft parts are isometric relative to crown volume. This assumption seems to hold true for comatulid crinoids (Brower, 1987). It is important to note that soft tissue occurs inside the calcite plates of the skeleton in the form of an organic matrix. Soft parts are also housed within the cavities enclosed by the aboral cup, anal tube, and arms. At any rate, the crown volume will serve as the measure of size and relative age for study of functional aspects of ontogeny. The volumes must be calculated because all of the crowns are pre-

served in matrix. The computations utilize the following approximations: frustum of a cone or tapering cylinder for aboral cup, anal tube, and column, and half of a cylinder with elliptical cross-section for the arm segments. The anal tube is typically enveloped by the arms, and its volume must be estimated from specimens that show the entire anal tube.

D. Food-gathering system characters (Table 6): (1) Total number of arm branches. (2) Number of plates in all arms. (3) Length of all arms. (4) Number of covering plates or food-catching tube-feet. (5) Food-gathering capacity. (6) Weighted average width of food groove. The last three characters need further discussion. As men-

tioned above, one primary or food-catching tube-foot is associated with each lappet or covering plate of modern crinoids, and this is believed to have been the case for *Cupulocrinus levorsoni*. Unfortunately, the insides of the arms with the food grooves are not always visible, and the two parameters must be computed. The height of a covering plate remains the same throughout development. The number of food-catching tube-feet for one arm segment can be calculated as follows: ([length of arm segment/average height of covering plate] times two). The multiplier (x2) is used because tube-feet are located on both sides of an arm. The number of food-catching tube-feet is then added for all arms to produce a total. A

Equation No.	X Variable	Y Variable	Exponent	Initial Intercept	Initial Intercept (logarithms)	Correlation Coefficient	Standard Error of Intercept (logarithms)	Standard Error of Exponent	Isometric Exponent	Student's <i>t</i>	No. of Specimens	Minimum X	Minimum Predicted Y	Maximum X	Maximum Predicted Y
1	Primibrachial height	Primibrachial width	2.21	2.02	0.306	0.903	0.0452	0.190	1.0	6.39**	25	0.394	0.257	0.850	1.41
2	Secundibrachial height	Secundibrachial width	2.33	1.80	0.254	0.828	0.0676	0.267	1.0	4.99**	24	0.400	0.212	0.725	0.849
3	Tertibrachial height	Tertibrachial width	2.72	2.14	0.331	0.837	0.0849	0.317	1.0	5.43**	22	0.408	0.187	0.685	0.765
4	Quartibrachial height	Quartibrachial width	2.88	2.53	0.403	0.781	0.118	0.392	1.0	4.79**	21	0.395	0.175	0.630	0.670
5	Quintibrachial height	Quintibrachial width	1.54	1.02	0.00821	0.748	0.111	0.308	1.0	1.75	11	0.325	0.181	0.586	0.448
6	Cup height	Primibrachial height	0.737	0.279	-0.554	0.837	0.0363	0.079	1.0	-3.33*	26	1.75	0.421	4.65	0.865
7	Cup height	Secundibrachial height	0.617	0.305	-0.516	0.806	0.0333	0.0731	1.0	-5.23*	25	1.75	0.431	4.65	0.787
8	Cup height	Tertibrachial height	0.563	0.303	-0.519	0.805	0.0320	0.0696	1.0	-6.27*	23	1.75	0.415	4.65	0.720
9	Cup height	Quartibrachial height	0.515	0.298	-0.527	0.727	0.0344	0.0754	1.0	-6.43*	22	1.75	0.397	4.65	0.657
10	Cup height	Quintibrachial height	0.709	0.210	-0.678	0.519	0.858	0.183	1.0	-1.59	11	2.10	0.356	4.65	0.625
11	Cup height	Primibrachial width	1.63	0.120	-0.920	0.907	0.0629	0.137	1.0	4.60**	25	1.75	0.300	4.65	1.48
12	Cup height	Secundibrachial width	1.43	0.114	-0.943	0.829	0.0734	0.163	1.0	2.61*	24	1.75	0.253	4.65	1.02
13	Cup height	Tertibrachial width	1.44	0.0935	-1.03	0.796	0.0857	0.186	1.0	2.36*	22	1.75	0.209	4.65	0.853
14	Cup height	Quartibrachial width	1.46	0.0795	-1.10	0.795	0.0886	0.194	1.0	2.39*	21	1.75	0.180	4.65	0.754
15	Cup height	Quintibrachial width	1.09	0.0924	-1.03	0.723	0.107	0.227	1.0	0.401	11	2.10	0.208	4.65	0.495

Table 4. Equation for growth of brachials in *Cupulocrinus levorsoni*. Student's *t*-test values that are significant at the 0.05 and 0.01 levels are indicated by asterisks (* and **, respectively).

Equation No.	X Variable	Y Variable	Exponent	Initial Intercept	Initial Intercept (logarithms)	Correlation Coefficient	Standard Error of Intercept (logarithms)	Standard Error of Exponent	Isometric Exponent	Student's <i>t</i>	No. of Specimens	Minimum X	Minimum Predicted Y	Maximum X	Maximum Predicted Y
1	Cup height	Cup volume	3.73	0.203	-0.692	0.970	0.115	0.276	3.0	2.66*	11	1.75	1.64	3.7	26.9
2	Cup height	Volume of one ray	6.1	0.056	-1.25	0.953	0.233	0.559	3.0	5.54**	11	1.75	1.70	3.7	163
3	Cup height	Crown volume	5.67	0.644	-0.191	0.975	0.158	0.380	3.0	7.02**	11	1.75	15.4	3.7	1070

Table 5. Equations for volumetric increase in *Cupulocrinus levorsoni* during growth. Student's *t*-test values that are significant at the 0.05 and 0.01 levels are indicated by asterisks (*) and (**, respectively).

similar technique is employed for the food groove widths. The ratio of food groove width/brachial width is independent of size and relative age, and the food groove width of an arm segment equals the ratio of food groove width/brachial width multiplied by the observed brachial or arm width. The weighted average is then derived for all arms. The food-gathering capacity is the total number of food-catching tube-feet times the average width of the food grooves (Brower, 1987; and discussion below). (7) Height of arm. This distance ranges from the radial facet to the distal tip of an arm. (8) Area spanned by the arms. As discussed above, the arm fan is thought to have been essentially planar or parabolic. The area is given by the area of an outer circle with a radius equal to half of the cup width plus the arm height less the area of an inner circle with a radius of half that of the cup width (Ausich, 1980). (9) Branch density. This

parameter is calculated by the number of arm branches divided by the area spanned by the arms during food-gathering (Ausich, 1980). (10) Tube-foot spacing or number of food-catching tube-feet per mm along one side of an arm (Meyer, 1979, 1982a, 1982b). This variable is half of the number of food-catching tube-feet divided by the length of the food-gathering system.

Growth of the aboral cup and anal tube

Thirty-five specimens with cup heights from 1.75 to 4.65 mm were used to determine the growth sequence of *Cupulocrinus levorsoni* (Plates 1-4; Figure 1). The plate structure of the cup is stabilized at all sizes and relative ages. Inasmuch as the cup consists of a rigid boxwork

Equation No.	X Variable	Y Variable	Exponent	Initial Intercept	Initial Intercept (logarithms)	Correlation Coefficient	Standard Error of Intercept (logarithms)	Standard Error of Exponent	Isometric Exponent	Student's <i>t</i>	No. of Specimens	Minimum X	Minimum Predicted Y	Maximum X	Maximum Predicted Y
1	Crown volume	Number of arm branches	0.450	11.0	1.04	0.886	0.137	0.0629	0.333	1.86	11	16.2	38.6	794	222
2	Crown volume	Number of brachials	0.732	66.8	1.82	0.975	0.107	0.0490	0.333	8.13**	11	16.2	514	794	8840
3	Crown volume	Length of arms	0.762	26.2	1.42	0.984	0.088	0.0404	0.333	10.6**	11	16.2	220	794	4260
4	Crown volume	Number of food-catching tube-feet	0.745	316	2.50	0.980	0.0963	0.0442	0.333	9.32**	11	16.2	2520	794	45800
5	Crown volume	Food gathering capacity	0.900	26.4	1.42	0.994	0.0623	0.0286	0.667	8.15**	11	16.2	325	794	10700
6	Crown volume	Food groove width	0.183	0.0729	-1.14	0.896	0.0532	0.0244	0.333	-6.16**	11	16.2	0.121	794	0.247
7	Crown volume	Height of arm	0.347	4.22	0.626	0.992	0.0282	0.0130	0.333	1.08	11	16.2	11.1	794	42.9
8	Crown volume	Area spanned by arms	0.678	68.9	1.84	0.994	0.0493	0.0226	0.667	0.501	11	16.2	456	794	6380
9	Crown volume	Branch density	-0.348	0.286	-0.544	-0.789	0.141	-0.0645	0.000	5.40**	11	16.2	0.108	794	0.0279

Table 6. Equations for growth of food-gathering parameters. Student's *t*-test values that are significant at the 0.01 level are indicated by asterisks (**).

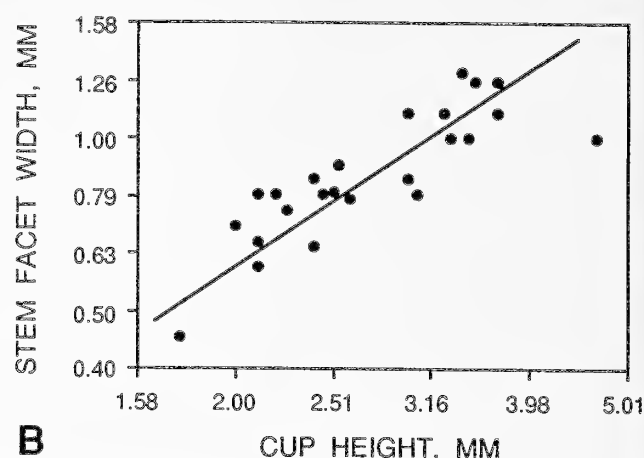
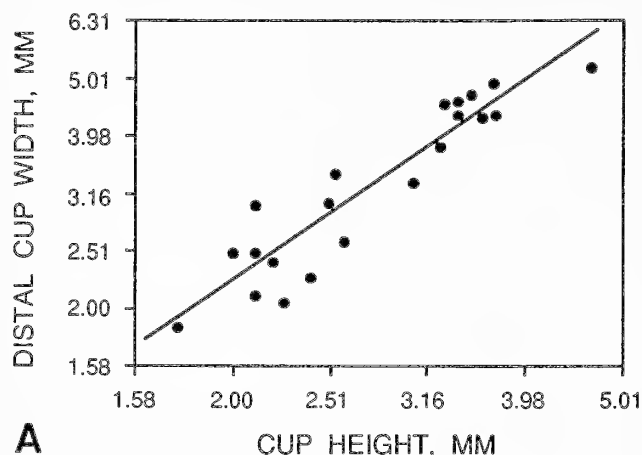


Figure 5. Graphs showing ontogeny of aboral cup for *Cupulocrinus levorsoni* Kolata. Equation data are in Table 3.

of plates, it is not surprising that most dimensions of the cup and its plates are isometric (Table 3). All cup parameters are linear dimensions, so the isometric exponents equal 1.0. The distal cup width (Y) is positively allometric with respect to its height (X) (Figure 5A; Table 3, equation 1). Thus width increases more rapidly than height, and the width/height ratio is greater in larger and older crinoids. Conversely, the

stem facet width (Y) versus cup height (X) exhibits isometry (Figure 5B; Table 3, equation 2). These differential ontogenetic trajectories dictate changes in the cup shapes of young and adult crinoids. The distal region of the cup with the radial plates becomes progressively wider compared to the cup height and column facet, so that mature cups are more broadly conical than juvenile ones (Plates 1-4; Figure 1). The

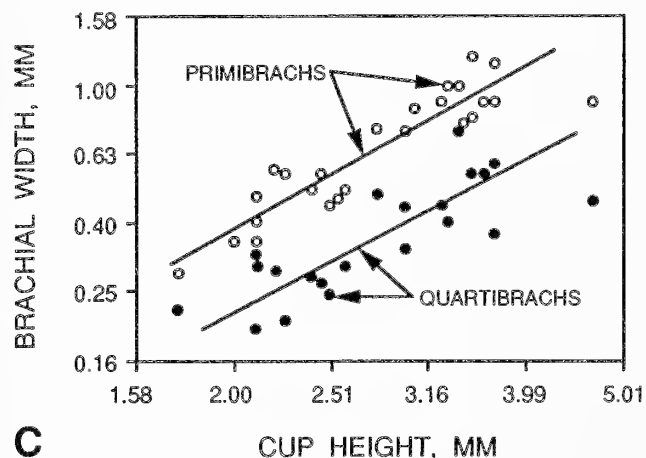
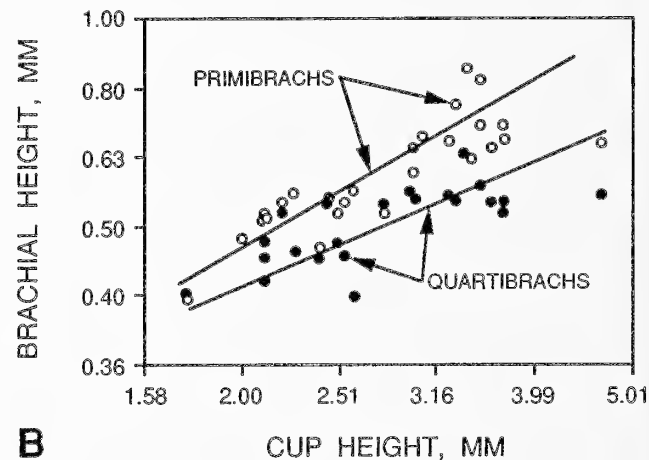
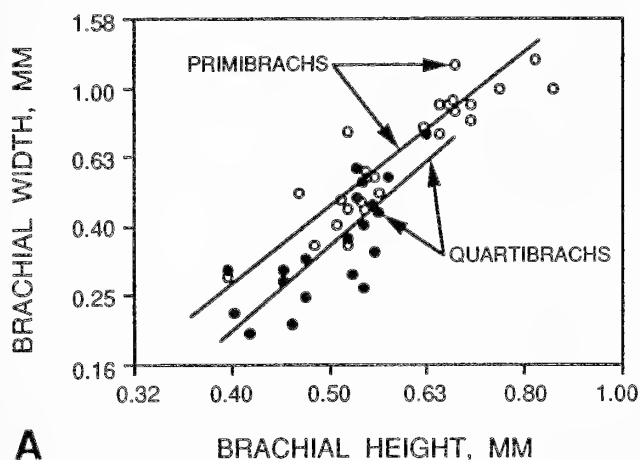


Figure 6. Graphs illustrating development of brachials for *Cupulocrinus levorsoni* Kolata. See Table 4 for equations.

infrabasals and basals retain roughly the same proportions of width to height at all sizes (Table 3, equations 3, 4). As expected, the width/height ratio of the radials increases during growth, and the relation is statistically significant at the 0.05 probability level (Table 3, equation 5). This enables the cup to accommodate the developing arms, and the radial facets occupy approximately 72% of the width of the plates in all specimens (Table 3, equation 6).

The preservation of several complete anal tubes yields some information about growth of this structure; anal tube growth is poorly known in fossil crinoids. Anal tubes of immature specimens range from 5.7 to 9.6 mm in height. The cup heights of these calices vary from 1.75 to 2.1 mm (Plate 2, figure C; Plate 4, figures A, B; Figure 1G). Although the specimens are flattened, the abanal side of the anal tube contains four or five crudely arranged columns of irregular plates; each column bears about thirty to thirty-four plates. The anal opening is surrounded by small and irregular plates at the distal end of the tube. The only preserved adult anal tube is 35 mm high in an individual, with a cup height of 3.7 mm (Plate 1, figure C). The medial and distal plates on the abanal side of the tube are grouped in six to ten columns, and about one hundred plates can be counted in a complete column. Two conclusions can be drawn about the plate development sequence of the anal tube. New columns presumably became intercalated between older ones as the anal tube was extended distally by the formation of new plates at or immediately below its terminus. During development, calcite accretion increased the size of plates that formed earlier.

Development of arm plates

The brachials of *Cupulocrinus levorsoni* show systematic changes throughout the arms. Proximal plates are large and comparatively wide with respect to height, but more distal plates are smaller and more elongate in shape (Plates 1-4; Figures 1H, I). Thus the higher brachials have juvenile outlines relative to plates near the cup. This is also seen in the regenerated arm in the center of the small specimen illustrated on Plate 3, figure A. The regenerated primibrachs and secundibrachs resemble more distal brachials of crinoids of equivalent size and age (compare with Plate 2, figures B and E; Plate 4, figure D). This gradient of change is consistent with the hypothesis that the various plates performed different functions. The proximal arm plates, primibrachs, secundibrachs, and, perhaps, tertibrachs in mature crinoids mainly gave support and transported food to the mouth, whereas more distal plates trapped most of the food particles.

The highest brachials (hexibrachs and septibrachs) are present only in several of the largest specimens because they are the last plates to form in the arms. Although few data are available, the shapes of these brachials are probably independent of the size of the crown.

The correlation coefficients between the cup height and the height and width of the other brachials (primibrachs through quintibrachs) range from 0.519 to 0.907, and almost all are significantly larger than zero (Table 4). Consequently, these parameters are interpreted as size-dependent. In addition, the brachials share consistent patterns and gradients of allometry. The width (Y) exhibits strong positive allometry compared to the height (X) of all brachials (Figure 6A; Table 4, equations 1-5). At all levels, brachial widths increase more rapidly than heights than in isometric crinoids, and the width/height ratios of all plates become larger with progressive age. The brachial heights and widths (Y) versus cup height (X) are characterized by negative and positive allometry, respectively (Figures 6B, C; Table 4, equations 6-15).

Although the differences between the equations are not statistically significant (tested by Student's *t*), the ontogenetic patterns are adjusted so that the more distal brachials possess slightly smaller width/height ratios than proximal plates of similar height (Figure 6A). Similarly, distal plates tend to be somewhat smaller than plates closer to the cup in any one specimen (Figures 6B, C). During growth, the new brachials develop at the distal tips of the arms, as discussed below. The differential allometric changes, in conjunction with the plate development sequence, interact to produce the changes in morphology of the brachials in various pads of the arms.

The brachial size increases by marginal deposition of calcite throughout ontogeny. The food grooves become wider and deeper in larger brachials of any one type, such as the secundibrachs. This is mainly due to calcite deposition along the sides of the brachials rather than resorption. Within a single crinoid, the widths of the food grooves decrease somewhat from proximal to distal plates (e.g., Plate 1, figure B). The ratio of food groove width/brachial width is stabilized for any one order of plates as shown by the following averages: primibrachs, 0.538; secundibrachs, 0.604; tertibrachs, 0.585; quartibrachs, 0.601; quintibrachs, 0.547; hexibrachs, 0.690; and septibrachs, 0.800. Thus the relative width of the food grooves generally increases in a distal direction. This situation is produced by the more distal brachials tapering more rapidly than their food grooves.

Because of the expansion of the food grooves, calcite accretion must also augment the width of the covering plates to prevent the formation of gaps. Conversely, the height of the covering plates is essentially constant after they are formed. Covering plates have the following average heights: primibrachs and secundibrachs, 0.252 mm; tertibrachs, 0.197 mm; quartibrachs, 0.187 mm; and quintibrachs through septibrachs, 0.180 mm. Distal covering plates are shorter than proximal ones. As the brachials become higher, new covering plates develop between older ones along the proximal and distal ends of the arm plates.

Aboral cup height and crown volume

The isometric exponent for a volume (Y) and a linear dimension (X) equals 3.0 (Table 2). The calculated exponents span an interval of 3.73 to 6.10, all of which are significantly greater than the isometric figure at probability levels of 0.05 or 0.01 (Table 5). The volumes increase much faster than would hold true for an organism with constant shape. The cup heights and crown volumes of complete specimens vary from 1.75 to 3.7 mm and from 16.2 to 794 mm³, respectively (Figure 7). Low variation is observed at all cup heights, and the large correlation coefficient of 0.975 denotes a high level of integration and coordination. It should be observed that the exponent for the volume of one ray (6.1) exceeds that for the cup volume, which is only 3.73. Consequently, the cup represents a decreasing fraction of the total volume in larger crowns as given by the following data: juvenile crinoid, cup volume 13.2%, anal tube volume 30.2%, and arm volume 56.6%; mature crinoid, cup volume 2.86%, anal tube volume 31.3%, and arm volume 65.8%. Because of the positive allometry, characters like the height of the aboral cup do not provide reasonable size variables. This point is often ignored in studies on allometry.

The volumetric contribution of the stem is uncertain because complete stems attached to crowns have not been preserved. The complete, or nearly complete, coiled column adjacent to paratype IGS 79P-22 has a volume of 5.34 mm³ (Plate 3, figure D; Plate 4, figure D). The stem diameter is similar to that of IGS 79P-22, which suggests that the crown

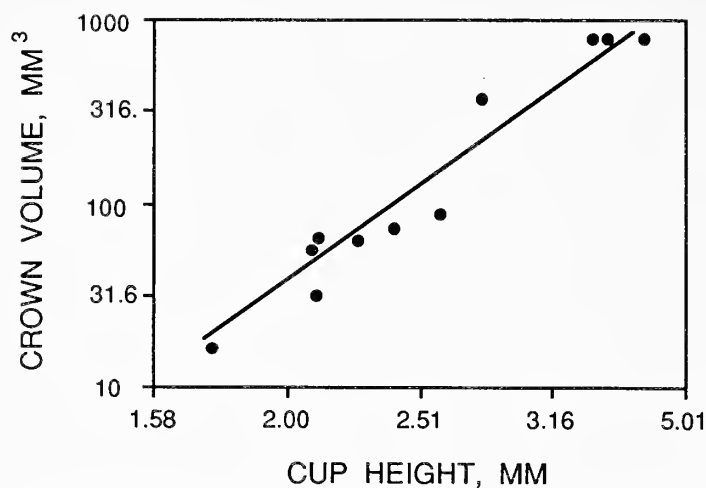


Figure 7. Graph for growth of aboral cup and crown volume in *Cupulocrinus levorsoni* Kolata. Equation data are in Table 5.

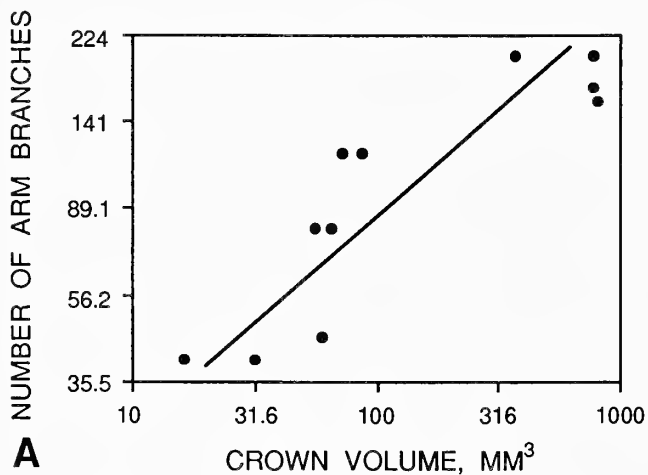
can be matched with the column, at least approximately. In this specimen, the stem volume equals 8.21% of a crown volume of 65.0 mm³. An incomplete column 50 mm long with a volume of 26.6 mm³ is joined to the partial crown of paratype SUI 50863 (cup height 3.4 mm). The crown volume of another specimen with equivalent cup height is

783 mm³. The incomplete stem makes up 3.40% of the crown volume. Although inconclusive, these figures clearly show that the column represents a minor fraction of the total volume of the animal.

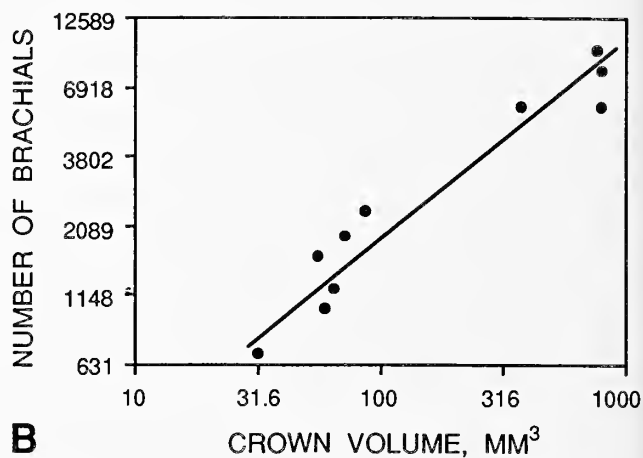
Size and capacity of the food-gathering system

Crinoids experience the problem shared by many filter- and suspension-feeders in that the food-gathering capacity is proportional to a linear dimension or area, but the tissue that must be fed increases as a volume or mass. In living and fossil crinoids, most food particles are caught by the primary or long tube-feet on the arms, but the volume of the soft parts is presumed to be isometric with, and proportional to, the crown volume.

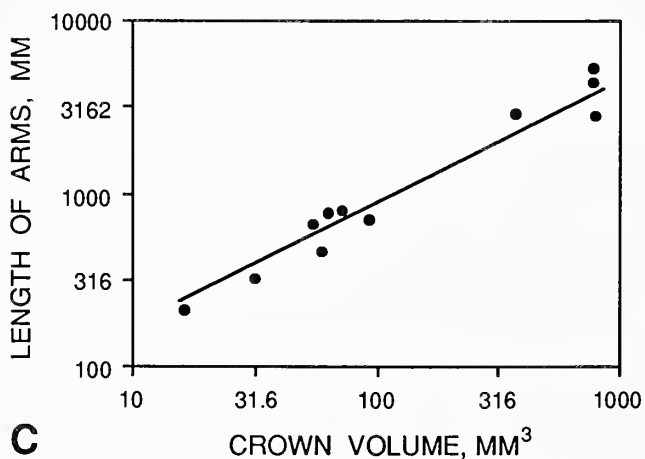
The number of arm branches rises with larger crown sizes (Plates 1-4; Figure 8A; Table 6, equation 1). The arms of the smaller specimens are well-developed, with eight branches in each ray and terminal quartibrachs. Adults possess as many as fifty branches in a ray with hexibrachs or septibrachs at the arm tips. It seems reasonable to suppose that the number of arms (Y) would increase as a linear dimension, whereas the crown volume (X) is a cubed function; thus, the corresponding isometric exponent is 0.33. Although the observed exponent is 0.45, the Student's *t* of 1.86 shows that the null hypothesis of isometry cannot be rejected.



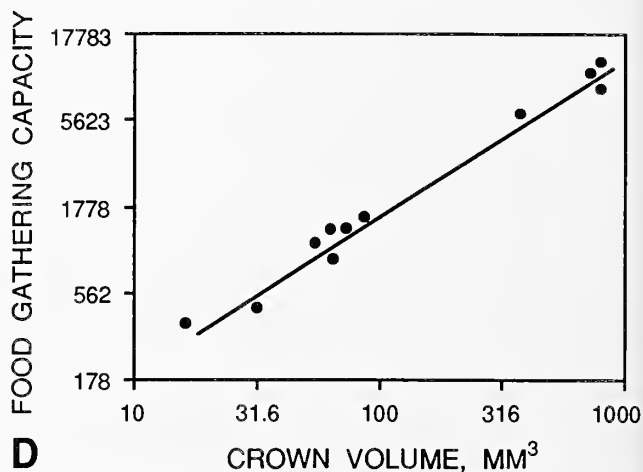
A



B



C



D

Figure 8. Graphs for ontogeny of crown volume and food gathering system of *Cupulocrinus levorsoni* Kolata. Equation data are given in Table 6.

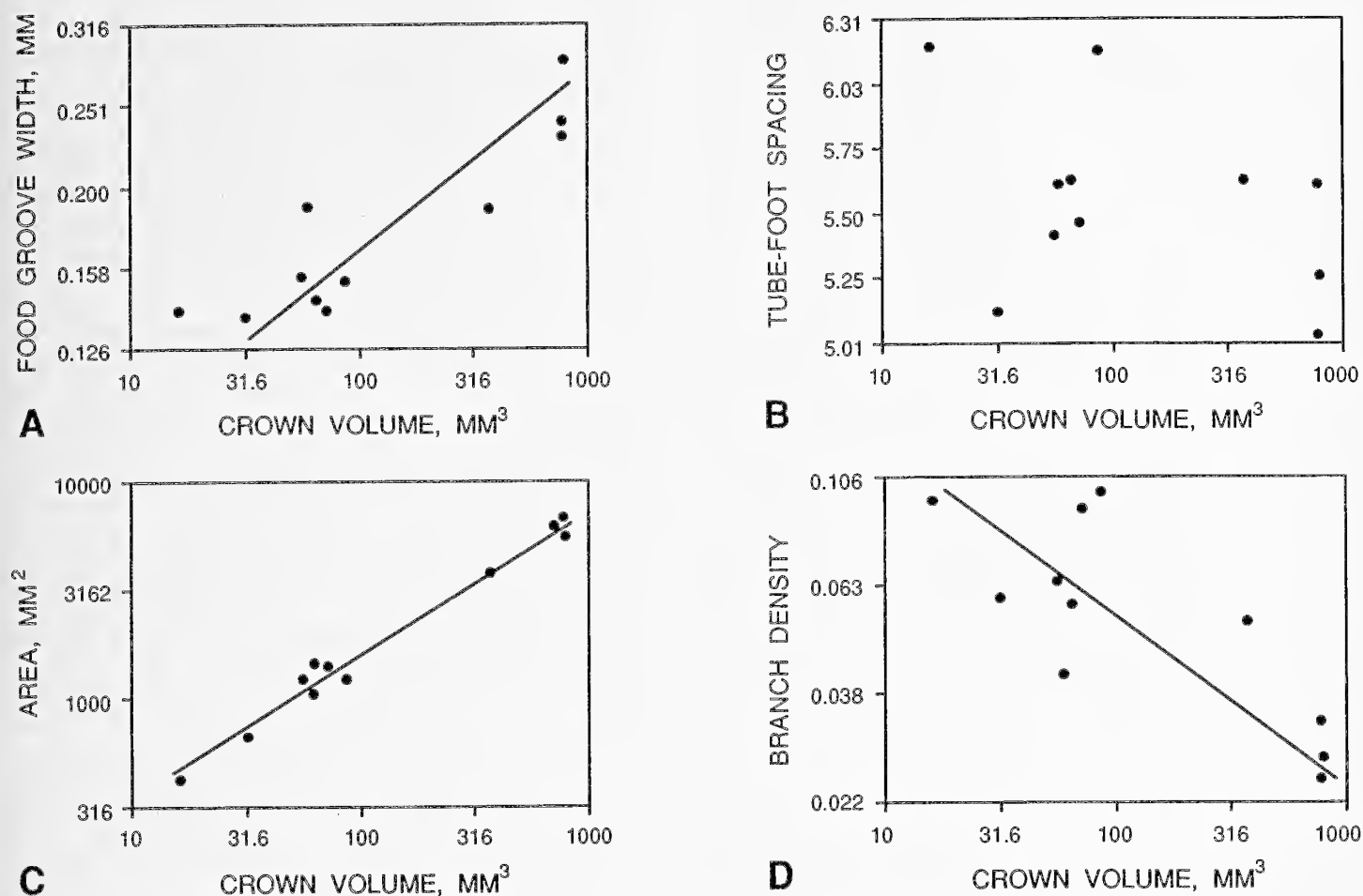


Figure 9. Graphs for crown volume and ecological niche parameters in *Cupulocrinus levorsoni* Kolata. Equation data are listed in Table 6.

The overall size of the arms is given by their length and number of brachial plates (Y). In a strict sense, both characters are linear dimensions. However, the volume of tissue is thought to be proportional to the crown volume (X). The exponent for an organism with constant shape would be 0.33. Extremely positive allometry is observed for both relationships in *Cupulocrinus levorsoni*, and the calculated exponents equal 0.732 and 0.762 (Figure 8B, C; Table 6, equations 2, 3). Clearly, the number of brachials and the length of the arms increase faster than if the data were isometric. Actually, the growth rates are squared compared to an isometric postulate. During development, new brachials are initiated at the distal tips of the arms as small, bullet-shaped terminal plates. Unlike the stem, new plates do not intercalate between the older ones. New branches appear in the arms whenever a terminal brachial develops into an axillary one. In short, with the addition of arm branches and formation of new plates at the end of each branch, the number of plates increases exponentially.

The arms become longer by the formation of new plates and deposition of calcite on plates that were initiated earlier. As discussed above, the growth rates for the brachials relative to the size of the cup are relatively slow. Therefore, the rate of production of new plates seems more important than the increase in height of the brachials in dictating the length of the arms.

The data for total arm length and number of brachial plates (Y) against crown volume (X) in *Cupulocrinus levorsoni* resemble those of Paleozoic disarid inadunate crinoids with ramules (Brower, 1987).

However, the exponents for these relationships in the cupulocrinid do not differ from those calculated by Brower (1973, 1974, 1978) for pinnulate camerate crinoids. This finding is most surprising, and the absence of pinnules does not seem to impose limits on the developmental rates of the arms.

One food-catching tube-foot is present below each covering plate. Inasmuch as the food is trapped mostly with these tube-feet, their number and distribution is critical to the animal. The pattern for number of food-catching tube-feet versus the crown volume and implied volume of tissue is very similar to the length and number of brachial plates in the arms (Table 6, equation 8).

Brower (1987) suggested that the food-gathering capacity of a crinoid could be approximated by the number of food-catching tube-feet multiplied by the width of the food grooves. The reasoning is that the number of food particles caught would depend on the number of tube-feet. As a result, the width of the food grooves would place an upper limit on the size of the food particles. The food-gathering capacity (Y) ought to scale as a square inasmuch as it is the product of two linear dimensions. Tissue volume is considered isometric with crown volume (X), a cubic function. The isometric exponent is 0.67. The observed relationship is positively allometric with an exponent of 0.900, and this is significantly larger than the isometric exponent at the 0.01 probability level. The food-gathering capacity of *Cupulocrinus levorsoni* increases more rapidly than predicted (Figure 8D; Table 6, equation 5). Note that the ratio of food-gathering capacity/crown volume declines from 20 to

13.5 over the developmental series. Older crinoids are characterized by relatively smaller food-gathering capacities than younger ones, and the decrease is statistically significant. If the ratio of food-gathering capacity/crown volume is constant regardless of size and age, the allometric equation would have an exponent of 1.0. Testing the calculated exponent of 0.900 against a population value of 1.0 with Student's *t*-test indicates a value of 3.57, which is significant at the 0.01 risk level. Brower (1987) published similar data for Ordovician and Mississippian calceocrinids, and this pattern may be typical for crinoids in general.

Growth of the ecological niche parameters

As noted above, morphological characters define two important aspects of the ecological niche for a suspension-feeding crinoid. These two aspects of the niche include elevation above the sea floor and food particle size. The pertinent data on elevation have been discussed. The food groove limits width and is a measure of the largest size of the food particles that can be processed. The exponent for the weighted average width of the food grooves (Y) plotted against crown volume (X) for a crinoid with no shape change during ontogeny would equal 0.33 (Table 2). The observed relationship is subject to marked negative allometry with an exponent of 0.183 (Figure 9A; Table 6, equation 6). Although the food grooves are wider in older and larger individuals, the rate of change is comparatively small, less so than for an isometric organism.

This is dictated by the progressive addition of arm branches throughout development because the new branches are more narrow than older and more proximal ones.

The correlation coefficient for crown volume (X) versus tube-foot spacing (Y) is only -0.416 with nine degrees of freedom; this does not differ from a postulated value of zero at the 0.05 probability level (Figure 9B). Clearly, the variables are independent, and the tube-foot spacing is the same regardless of size. The tube-foot spacing must reflect the patterns of water flow in the vicinity of the tube-feet, and the tube-foot spacing of Recent crinoids is correlated with environment and food-catching habits (Meyer, 1979, 1982a). The average tube-foot spacing of *Cupulocrinus levorsoni* is 5.56 tube-feet per mm with a standard deviation of 0.350; this falls well within the range of 4.59 to 9.49 tube-feet per mm that was determined by Meyer (1979, 1982a) for extant comatulid crinoids. This indicates that living and fossil crinoids are similar with respect to food gathering.

The height of the arms (distance from radial facet to the arm tip) and the area of water spanned by the arms (Y) both increase with respect to the calyx volume (X) in larger animals. The calculated exponents of 0.347 and 0.678 are nearly identical to those expected for isometric scaling (i.e., 0.33 and 0.67, respectively (Figure 9C; Table 6, equations 7, 8)). The smallest and largest areas constitute 424 and 6820 mm², respectively. B.M. Hand of Syracuse University (personal commun., 1990) estimated that the current velocity for the area inhabited by *Cupulocrinus levorsoni* ranged from 10 to 20 cm per second. Even with

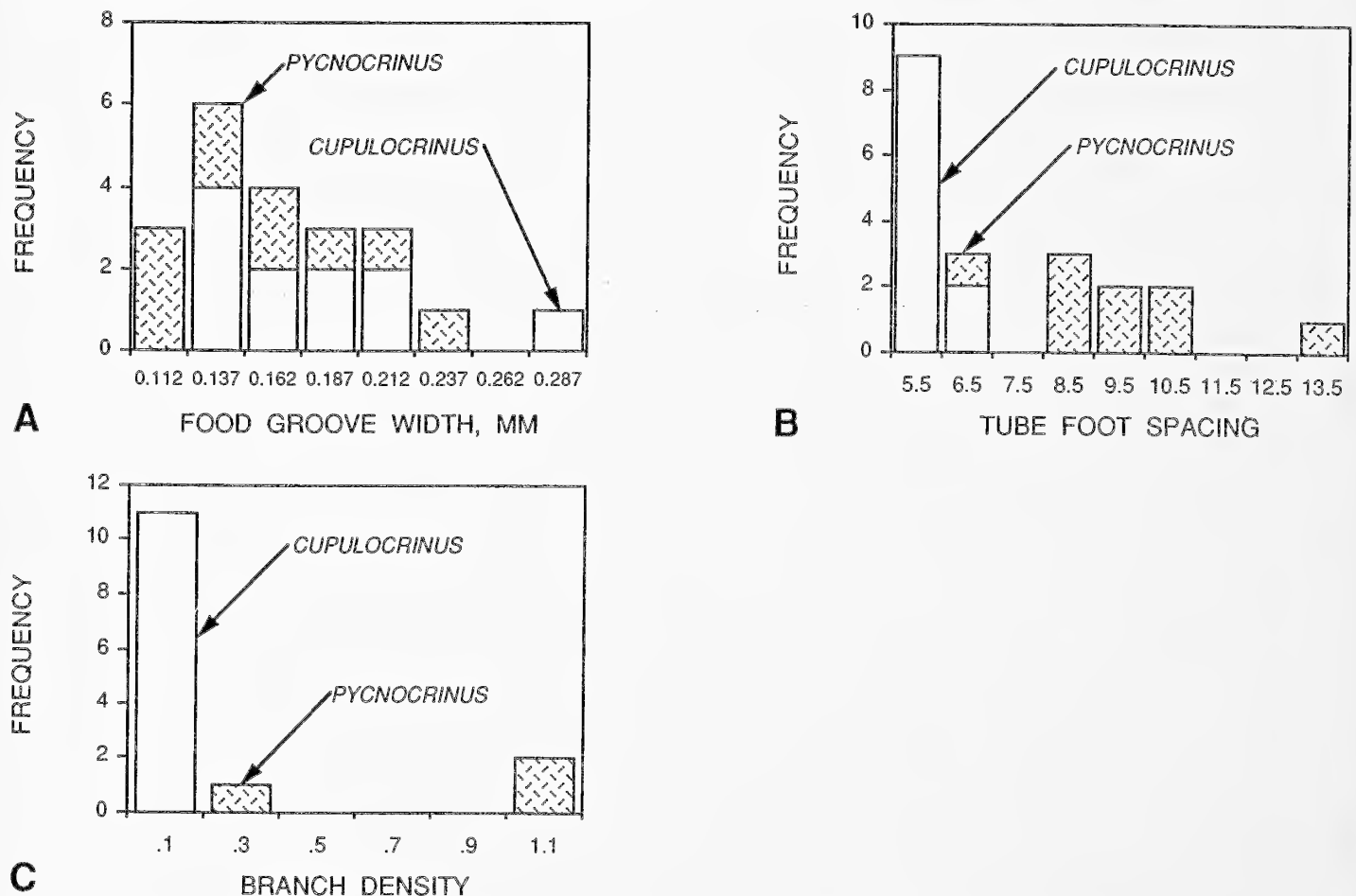


Figure 10. Histograms showing comparison of food-gathering systems of *Cupulocrinus levorsoni* Kolata and *Pycnocrinus gerki* Kolata.

these relatively small current velocities, both juvenile and adult crinoids must have filtered prodigious amounts of water. Recent crinoids living in shallow water are typically nocturnal (Macurda and Meyer, 1983), and it seems reasonable to suggest a feeding period of eight hours during which $1,830,000 \text{ cm}^3$ (small individuals) and $29,500,000 \text{ cm}^3$ (largest adults) of water would have flowed through the expanded arms at a current velocity of 15 cm per second. The length of the cylinder of water moved through the arms during this time interval would equal 4.32 km.

The branch density is given by the number of arm branches divided by the area spanned by the arms during food gathering. This variable illustrates the overall structure of the arms as a filter (Ausich, 1980). If the ratio were independent of size, an exponent of zero would occur for branch density (Y) versus crown volume (X). The observed exponent of -0.348 indicates that branch density becomes smaller in larger animals (Figure 9D; Table 6, equation 9). Thus the arm branches of older crinoids are more widely dispersed within the area of water filtered than in smaller specimens. It should be observed that this affects the validity of using a circular arm fan to calculate the area of water spanned and filtered by the arms. This geometric approximation becomes less adequate with progressively smaller branch densities. The branch density also depends on the size and crown volume of *Cupulocrinus levorsoni*. Basic geometry implies that this should also generally hold true for other crinoids.

Brower (In press) has studied the development of two other typical cupulocrinids from the slightly younger Dunleith Formation (Galena Group) of northern Iowa and southern Minnesota. *Cupulocrinus levorsoni* is characterized by longer and more slender arms, more narrow food grooves, and higher branch densities than in most other cupulocrinids of the same size and relative age. As discussed above, the overall similarities of arm geometry suggest that the feeding habits of *C. levorsoni* are more similar to those of many dendrocrinids than cupulocrinids.

Food-gathering parameters for *Cupulocrinus levorsoni* and *Pycnocrinus gerki*

Although the specimens of *Pycnocrinus gerki* are not suitable for the study of ontogeny, some comparisons can be made with *Cupulocrinus levorsoni*. The columns of the pycnocrinids are generally longer than those of the cupulocrinids; this suggests that the two species fed at different levels. Unfortunately, this cannot be documented conclusively because of the lack of complete stems and the fact that *C. levorsoni* may have wrapped its stem around an object that was elevated above the seafloor.

In addition, the food-gathering systems of the two crinoids contrast markedly. The arms of *Cupulocrinus levorsoni* branch isotomously numerous times, but the pycnocrinids bear four pinnulate arms in each ray (compare Plates 1-4 with Plate 5). *Cupulocrinus levorsoni* probably trapped most food items with the distal parts of the arms, and the more proximal brachials conveyed the food to the mouth. Based on analogy with Recent crinoids, one would expect that most food particles were taken by the food-catching tube-feet located on the pinnules of *Pycnocrinus gerki*, and that the arms provided the transport system toward the mouth.

The similarities and differences were investigated with Mann-Whitney U-tests. The incomplete nature of the data precludes any multivariate statistics. The food groove widths of the two forms intergrade,

and food particles of similar sizes were probably taken. The Z value corresponding to the Mann-Whitney U equals 1.27, which is not significant at the 0.05 probability level (Figure 10A). Conversely, the tube-foot spacing and branch densities of the species are almost completely separate (Figure 10A, B). The Z values, -3.61 and -2.57 for tube-foot spacing and branch density respectively, demonstrate that the null hypothesis of no difference should be rejected at the 0.01 level. *Pycnocrinus gerki* has more closely spaced tube-feet and greater branch densities because of its pinnulate arms. It is significant that the tube-foot spacings of *Cupulocrinus levorsoni* (5.04 to 6.18 tube-feet per mm) are most similar to living, deeper-water, comatulids that have values ranging from 4.59 to 6.62 tube-feet per mm (Meyer, 1979). Meyer inferred that these species capture food by motile particle collection and perhaps gravitational deposition. On the other hand, the tube-foot spacings of the pycnocrinids vary from 6.09 to 14.1 tube-feet per mm. This range of spacings overlaps and exceeds the 7.18 to 9.49 tube-feet per mm calculated by Meyer (1979) for living species from more agitated areas with unidirectional current flow where the food is thought to be gathered by direct interception and inertial impact. Several possible explanations can be offered, none of which are mutually exclusive. The food-catching techniques of the two species may have differed. *Pycnocrinus gerki* may have utilized inertial impact and direct interception, whereas *Cupulocrinus levorsoni* may have utilized motile particle collection and gravitational deposition. Alternatively, differences in current velocities may have been involved. Inasmuch as current velocity typically increases with elevation above the seafloor, *Pycnocrinus gerki* may have fed higher above the sediment in a regime of stronger currents. In addition, the pycnocrinid might have fed during more agitated intervals, whereas the cupulocrinid may have been active at times of quieter water. At any rate, the two crinoids were ecologically separated.

Acknowledgments

We thank D.R. Kolata and R. Norby of the Illinois Geological Survey (IGS) and J. Golden of the University of Iowa (SUI) for the loan of specimens. D.R. Kolata kindly provided stratigraphic data and paleoecological insights. The manuscript was reviewed by T.W. Broadhead of the University of Tennessee, E. Landing of the New York State Geological Survey, and G.C. McIntosh of the Rochester Museum and Science Center. This research was supported by National Science Foundation grant EAR 89-03960. Syracuse University furnished \$200 toward publication of this report.

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Biostratigraphy and biogeography of Late Silurian–Early Devonian echinoderms

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Abstract

Several years of detailed collecting have shown the echinoderm fauna of the Decatur Limestone and Ross Formation of west-central Tennessee to be much more diverse than previously reported. Collectively, this fauna of sixty-nine species referable to thirty-eight genera and seven classes spans the Silurian–Devonian boundary and shows a gradual pattern of taxonomic “turnover” at the boundary. In addition to providing the precise stratigraphic ranges of many Decatur/Ross taxa, collections of this interval expand both the stratigraphic and geographic ranges of many echinoderm genera. Overall, the composition of the fauna at the generic level is most similar to that of the Hunton Group of Oklahoma, followed by Bohemia and western France. Lower levels of similarity exist between Tennessee and coeval faunas of New York, Missouri, and Maryland. Strongest similarity at the generic level between Tennessee and Oklahoma is shown by camerate crinoids, whereas similarities to European sections are strongest among disparid “inadunate” and flexible crinoids. This suggests possible differences in larval ecology among major crinoid groups.

Introduction

Rocks of Late Silurian and Early Devonian age have been studied extensively, and the Silurian–Devonian system boundary was the first major stratigraphic boundary to be formalized by international agreement (Martinsson, 1977). Because they have played such an important part in boundary definition and correlation, biostratigraphically important groups of organisms, especially graptolites and conodonts, are well-understood taxonomically and stratigraphically on virtually a global scale. Earlier studies of the distribution of echinoderm remains from this interval have focused on a regional scale (e.g., Podolia [Stukalina, 1977], Bohemia [Prokop, 1987], and Brittany [Le Menn, 1985]). Broader syntheses (Witzke et al., 1979; McIntosh and Macurda, 1981; Sevastopulo et al., 1989) based predominantly on published reports have not added to the empirical data base, but have presented generalizations of stratigraphic and geographic distributional patterns.

The Silurian–Devonian boundary interval in west-central Tennessee is especially important because it is well-documented in terms of both biostratigraphic zonation (McComb and Broadhead, 1980; McComb, 1987; Cappacioli, 1987) and interpretation of sedimentary environments (Gibson, 1988; Broadhead et al., 1989). Thus the stratigraphic significance of its diverse echinoderm fauna has been greatly enhanced.

This study highlights the details of local stratigraphic ranges in an environmental context and in terms of a regional and global significance.

Geologic setting

Upper Silurian (Pridolian) and Lower Devonian (Lochkovian) marine sedimentary rocks are exposed in a narrow outcrop belt in the western valley of the Tennessee River in west-central Tennessee (Figure 1). This area has been interpreted by Gibson et al. (1988) to have been a small area of stable marine shelf that was bounded on the (present day) north and west by the Reelfoot Rift system, on the east by the Nashville Dome, and on the south by the incipient Black Warrior

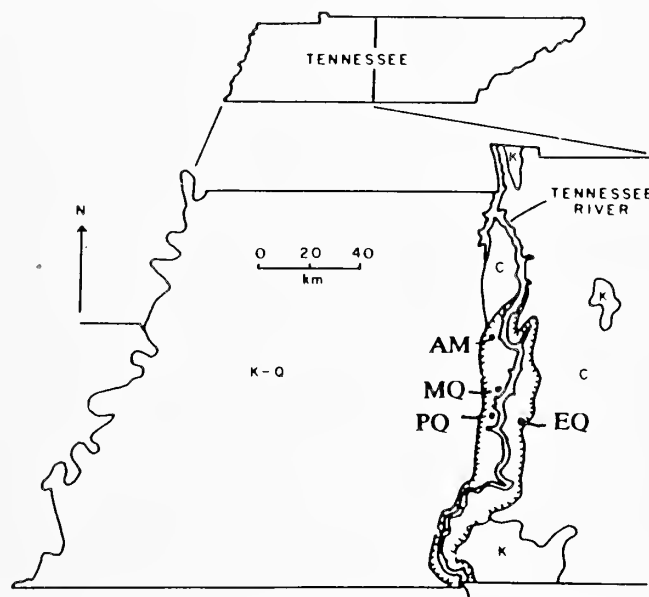


Figure 1. Outcrop area of Upper Silurian–Lower Devonian rocks (hatched area) in the western valley of the Tennessee River in west-central Tennessee. Silurian–Devonian strata are unconformably overlain by rocks of Carboniferous (C), Cretaceous (K), and Cretaceous through Quaternary age (K–Q) along the margins of the outcrop belt. Principal collecting localities referred to here are all quarry exposures: Allen's Mill (AM), Elkins Quarry (EQ), McClanahan's Quarry (MQ), and Parsons Quarry (PQ).

Basin. Paleogeographically, this shelf ("Ross Shelf" of Gibson et al., 1988) lay at approximately 25° south latitude (Figure 2) in an area subject to the influence of westerly storms.

Mixed carbonate and fine-grained siliciclastic sediment accumulated on this shelf throughout much of the Silurian (Barrick, 1983). By the Late Silurian (Pridolian), the shelf was dominated by echinoderm-rich, but relatively mud-poor, sediment that formed the skeletal packstone and grainstone beds of the Decatur Limestone. The lowest stratigraphic appearance of the conodont *Icriodus woschmidtii* Ziegler, at about the Silurian–Devonian boundary (see Broadhead et al., 1989), occurs in the upper 3.0 m of the Decatur Limestone in northern exposures, but in the lower Ross Formation in southern exposures. The Decatur Limestone is overlain by the Ross Formation (Lower Devonian), a lithically heterogeneous carbonate and shale unit which is divided into four members. Of these, only the Rockhouse Limestone at the base and the overlying Birdsong Shale are sufficiently well-exposed to provide extensive collections. These members are geographically restricted to the northern part of the outcrop belt, which also contains the best exposures of the Decatur Limestone.

During deposition of the Decatur and Ross Formations (maximum combined thickness of 45 m in the study area), the Ross Shelf was frequently disturbed by major storms. These storms influenced not only the basic succession of lithic types but also the preservation of echinoderms. The presence of large-scale cross-bedding, absence of abundant mud, and localized concentration of well-preserved, articulated echinoderms in the Decatur Formation suggest deposition well within the reach of scouring and winnowing by storms. The Rockhouse Limestone member of the Ross Formation is dominantly composed of beds of skeletal packstone separated by shale partings that become thicker and more numerous toward the top, where the Rockhouse Limestone grades into the Birdsong Shale. The Birdsong Shale becomes increasingly shaly near the top, where skeletal packstone beds again become common.

Biostratigraphy

Applications of echinoderm distributional data to biostratigraphic correlation are poorly developed, particularly in the Paleozoic (see

Broadhead, 1980, for summary). This is due largely to taphonomic disruption of echinoderm skeletal remains and the resulting difficulty in the identification of either isolated or small articulated groups of ossicles. Few taxonomically characteristic ossicles occur in the Silurian–Devonian boundary interval biota. Disaggregated and washed shale samples of the Decatur and Ross formations yield diagnostic plates, in addition to crinoid calyx fragments and thecae of juvenile crinoids, but the vast majority of disarticulated ossicles, including columnals, are not identifiable below the class level. Overall, however, the stratigraphic distribution of echinoderms within the Decatur Limestone and Ross Formation is distinctive (Table 1), and many occurrences in these rocks represent extensions of the known ranges of several genera and species.

Well-preserved and identifiable echinoderm remains are stratigraphically localized within the Decatur Limestone and Ross Formation, and the stratigraphic distribution data are summarized herein mostly in terms of generalized lithic or environmental unit subdivisions of each formation (see McComb, 1987; Reid, 1983). Each unit recognized in this study is characterized by an assemblage of echinoderm species, some of which are restricted to that unit (Table 1). Although most of the echinoderm species reported in this study were found during field work, several were recovered only from disaggregated and sieved (25 mesh) residues of shale samples (Table 2). Of particular importance are the biogeographically important cyclocystoid *Sievertsia* sp. and the crinoid *Pygmaeocrinus* sp. Small crinoid specimens found in the smaller size fractions (60 and 120 mesh sizes) represent the "kallimorphocrinoid" and "aidemocrinoid" ontogenetic stages of a disparid allagecrinacean, herein referred to "*Kallimorphocrinus*" sp.

Ranges of echinoderm species within the Decatur Limestone and Ross Formation

The Decatur Limestone has a fauna of twenty-eight species (seventeen genera), of which nineteen species (belonging to twelve genera) locally occur only within this formation. Most specimens come from two prominent, widespread, 2.0 m-thick beds of coarse-grained echinoderm packstone. The lower of these ("lower Decatur" of this report) is approximately 9.0 m below the Decatur–Ross contact, and the upper bed ("upper Decatur" of this report) is approximately 1.5 m below the

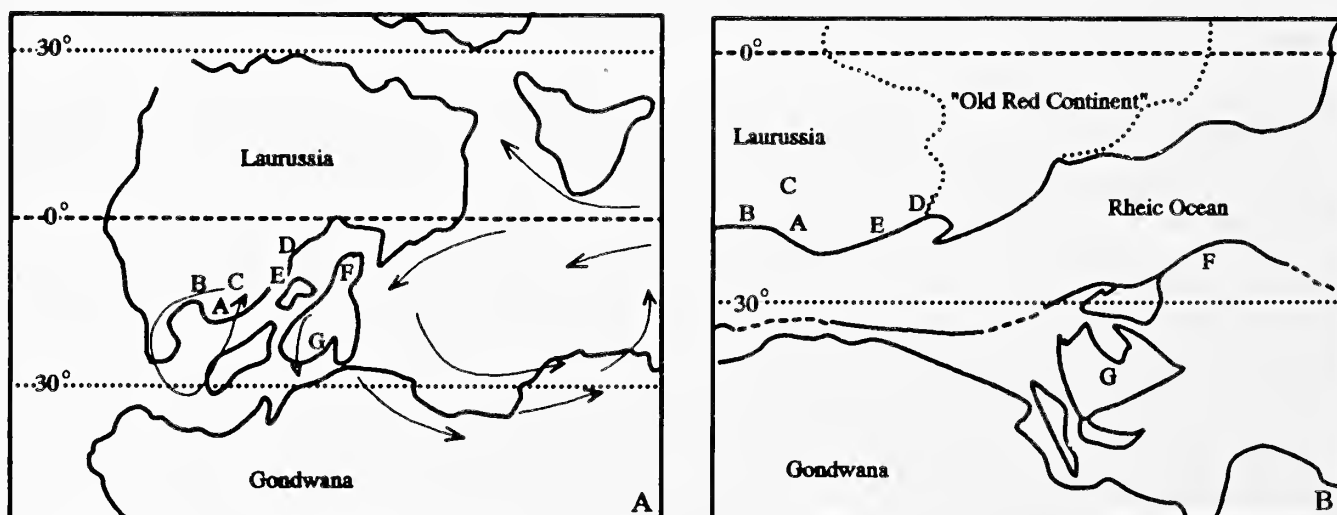


Figure 2. Paleogeographic reconstructions. A, From Barrett (1985), showing inferred warm ocean currents. B, From Morzadec et al. (1989). Locality designations: A-west-central Tennessee, B-Oklahoma, C-Missouri, D-New York, E-Maryland, F-Bohemia, G-Armorica.

SPECIES	Decatur		Rockhouse		R/B	Birdsong		
	L/M	U	L	U		L	Br	By
CRINOIDEA								
Camerata								
"Siphonocrinus" dignis	X							X
Elpidocrinus tholiformis		X						
Eudimerocrinus n. sp.		X	X					
Dimerocrinites n. sp.								X
D. sp. A								X
Lampteroocrinus tennesseensis		X						
Stiptocrinus benedicti		X						
S. nodosus	X	X						X
Hexacrinites adaensis		X						
H. carinatus	X	X	X					
Scyphocrinites elegans		X						
S. pratteni					X			
S. stellatus		X	X	X	X	X		
Eucalyptocrinites pernodosus	X							
E. sp. A	X							
E. sp. B		X						
E. sp. C		X						
E. sp. D	X							
Macrostylocrinus cf. laevis			X					
M. cf. pustulosus			X					
M. n. sp.			X					
Marsupioocrinus excavatus	X							
M. tennesseensis	X							
M. n. sp.								X
Marsupioocrinidae n. gen., n. sp.	X							
Patelloocrinacea n. gen. A, n. sp.			X					
Patelloocrinacea n. gen. B, n. sp.							X	
Dolatocrinus helderbergensis								X
Disparida								
Theloreus americanus, n. comb.			X	W	W	W	W	X
Eohalysiocrinus n. sp. A			X	W	W	W	W	X
Eohalysiocrinus n. sp. B					X			X
Pisocrinus sphaericus	X	X						
P. sp. A	X	X						
Crinobrachiatus sp.			X			W		X
Myelodactylidae sp.		X	W	W	W	W	W	X
"Kallimorphocrinus" sp.					W		W	W
Pygmaeocrinus sp.							W	
Cladida								
Thalamocrinus ovatus		X	X					X
T. elongatus			X					X
T. cf. robustus			X					
"Kooptoonocrinus" borealis								X
Flexibilia								
Lecanocrinus lawsonae						X		
L. meniscus			X		X			X
L. pisiformis	X	X	X					
L. cf. pusillus		X	X					
L. sp. A			X					
Ichthyocrinus n. sp.			X					
Nipteroocrinidae n. gen., n. sp.		X						
Edriocrinus adnascens			X		X		X	
Edriocrinus cf. pyriformis			X					
BLASTOIDEA								
Leptoschisma lorae							W	X
Polydeltoideus enodatus	X	X						
Phaenoschismatidae n. gen., n. sp.								X
RHOMBIFERA								
Tyrridiocystis chelyon							X	
EDRIOASTEROIDEA								
Pyrgocystis sp.			X					
CYCLOCYSTOIDEA								
Sievertsia sp.				W	W	W	W	W
ECHINOIDEA								
Echinocystitoidea indet.			W		W	W	W	X
STYLOPHORA								
Placocystitinae n. gen., n. sp.							W	X

Table 1. Generalized composite stratigraphic distribution of echinoderm species in the Decatur Limestone and Ross Formation, west-central Tennessee. Specimens were recovered from localities indicated in Figure 1. X=Specimen collected from outcrop. W=Specimen collected from disaggregated and washed shale sample.

SPECIES	AM	PQ	MQ	MQ	MQ	MQ	MQ	MQ	MQ	MQ	MQ	MQ	MQ	MQ	MQ	PQ	EQ
	IR	uR	0.0	0.2	1.6	3.7	6.6	9.1	11.0	13.0	13.6	14.0	14.2	14.9	uB	uB	
CRINOIDEA																	
"Siphonocrinus"																	
dignis						X								X	X		
Scyphocrinites																	
sp.	X	X	X		X	X							X?				
Theloreus																	
americanus	X	X	X	X	X		X			X	X		X				
Eohalysiocrinus																	
n. sp.	X	X	X	X	X	X	X	X	X	X	X	X			X	X	
Crinobrachiatus																	
sp.					X												
Myelodactylidae																	
sp.	X	X	X	X	X		X			X	X	X	X		X	X	
"Kallimorphocrinus"																	
sp.											X						
Pygmaeocrinus																	
sp.									X	X	X						
Lecanocrinus																	
sp.															X		
Edriocrinus																	
adnascens				X		X	X										
Flexibilia																	
brachial plate					X							X					
hyperpinnulate																	
brachial plate	X	X	X	X	X	X	X		X	X	X	X	X		X		
BLASTOIDEA																	
?Leptoschisma																	
lorae	X				X			X								X	
CYCLOCYSTOIDEA																	
Sievertsia																	
sp.	X	X	X	X	X		X	X	X	X	X		X	X			
ECHINOIDEA																	
Echinocystitoidea																	
indeterminate	X		X		X			X						X		X	
STYLOPHORA																	
Placocystitinae																	
n. gen., n. sp.					X					X		X	X				

Table 2. Composite distribution of identified echinoderm remains from disaggregated shale samples from the Ross Formation. Allen's Mill (AM) was sampled only in the lower Rockhouse Limestone member. Parsons Quarry (PQ) was sampled both in the upper Rockhouse Limestone member and in the "bryozoan zone" of the upper Birdsong Shale member. McClanahan's Quarry (MQ) was sampled throughout a 15 m-thick continuous exposure of the Birdsong Shale member—numbers indicate height in meters above the base of the Birdsong. Elkins Quarry (EQ) was sampled only from the top of the "bryozoan zone" of the Birdsong Shale member. Average sample mass was approximately 1 kg.

same contact. Both packstone beds are below the first appearance of *Icriodus woschmidti* and are therefore considered to be Pridolian in age. Most of the Decatur Limestone is finer-grained than these beds and contains fewer identifiable remains.

Earlier studies of echinoderms from the Decatur Limestone reported only five species of camerate crinoids and one species of disparid crinoid (Springer, 1926). Four of these (Table 3) have not been observed in the field by the authors, and their precise stratigraphic occurrence is unknown. The Decatur Limestone is dominated by camerate crinoids with a total of twenty-one species (nine species in the lower and middle Decatur, eleven species in the upper Decatur). Lobolith fragments of the camerate *Scyphocrinites* are common throughout the Decatur, although identifiable calyces occur only in the upper part.

All eight species of *Eucalyptocrinites* in this and earlier studies are confined to the Decatur Limestone. Despite their apparent adaptability to muddy conditions (i.e., in the Waldron Shale), no specimens of *Eucalyptocrinites* are known from the Ross Formation. This is true even in the mud-poor skeletal packstone beds of the upper Birdsong Shale (bryozoan zone), which represent a waning of the siliciclastic mud influx that otherwise characterizes the Birdsong Shale. This suggests extinction of *Eucalyptocrinites* species very near the Silurian-Devonian

boundary in west-central Tennessee, although *Eucalyptocrinites* continued to survive in central Europe into the early Middle Devonian.

Other echinoderms in the Decatur Limestone include a few species of disparid, cladid, and flexible crinoids and a single blastoid species (Table 1). Species of the disparid crinoid genus *Pisocrinus* do not occur above the Decatur Limestone, a pattern similar to that of *Eucalyptocrinites* (Table 1).

The Rockhouse Limestone member (Lower Devonian) of the Ross Formation overlies the Decatur Limestone (Upper Silurian) and differs from it primarily in being more thinly bedded with thin shale interbeds. The Rockhouse Limestone also contains abundant glauconite and a diverse and abundant brachiopod fauna. The lower Rockhouse Limestone contains a diverse echinoderm assemblage (twenty-two species, fifteen genera), which lacks a dominant crinoid component and is composed of nearly equal proportions of camerate, disparid, cladid, and flexible crinoids. This local reduction in the diversity of camerates may reflect an intolerance to increased amounts of fine siliciclastic sediment. A more dramatic but similar example of reduced camerate abundance and diversity may have occurred during the Middle Carboniferous (Waters et al., 1982). Seven crinoid species occur in both the lower Rockhouse Limestone and Decatur Limestone, and nine

SPECIES	Decatur	Ross
Camerata		
<i>Gazacrinus stellatus</i>		X
<i>Scyphocrinites spinifer</i>		X
<i>Eucalyptocrinites occidentalis</i>	X	
<i>E. sculptilis</i>	X	
<i>E. sp. E</i>	X	
Disparida		
<i>Cremacrinus decatur</i>	X	
<i>Myelodactylus schucherti</i>		X
Flexibilia		
<i>Ichthyocrinus devonicus</i>		X
<i>Edriocrinus dispansus</i>		X
<i>E. explicatus</i>		X
<i>E. occidentalis</i>		X

Table 3. Earlier reported crinoid species from the Decatur Limestone and Ross Formation that lack more precise stratigraphic documentation.

species are restricted to the lower Rockhouse Limestone. Important crinoid genera that are most diverse in the lower Rockhouse Limestone include the camerate *Macrostylocrinus*, the cladid *Thalamocrinus*, and the flexible *Lecanocrinus*. Only eight species with a lowest occurrence in the lower Rockhouse Limestone continue into the Birdsong Shale.

The contact between the Rockhouse Limestone and the overlying Birdsong Shale is difficult to distinguish at most localities. The shale beds of the upper Rockhouse Limestone become increasingly thicker upwards, and the top of this member is placed at the horizon where limestone beds generally cease to dominate. Where there is no obvious distinction, an informal "upper Rockhouse–lowermost Birdsong" interval has been recognized (Clement, 1989). This interval has a relatively species-poor echinoderm assemblage. Eleven species (nine genera) were found in the upper Rockhouse Limestone or upper Rockhouse–lowermost Birdsong (Table 1), but camerate crinoids are restricted to species of *Scyphocrinites*. A specimen of *Scyphocrinites stellatus* (Hall) found in the lowermost Birdsong Shale at McClanahan's Quarry (MQ) represents the highest occurrence of that genus noted in this study. No scyphocrinitid is known from the bryozoan zone of the Birdsong Shale, although this interval is lithologically and faunally similar to the lower Rockhouse, which is replete with *Scyphocrinites* remains. It seems likely that this genus became extinct in Tennessee during the time of the deposition of the brachiopod zone of the Birdsong Shale, the approximate time of the worldwide extinction of *Scyphocrinites*.

The brachiopod zone of the Birdsong Shale is the extremely shaly middle part of the member (sensu Gibson, 1988). This interval contains a sparse but taxonomically diverse (eleven species, eleven genera) assemblage of echinoderms. Most specimens are at least partly disarticulated, and an effective means of sampling the brachiopod zone has been to disaggregate shale samples (Tables 1, 2). Remains of only a single camerate crinoid have been found in the brachiopod zone, and the species-level diversity is dominated by small disparid crinoids. The flexible crinoid *Edriocrinus adnascens* Dunbar, which typically cemented itself to a hard substrate (e.g., brachiopod valves), occurs commonly in this zone, but has not been found higher in the Birdsong Shale. Isolated plates of the disparid crinoid *Pygmaeocrinus* sp. were found in disaggregated shale samples from the uppermost shale bed of the brachiopod zone; this is the first report of that genus from North America.

The upper part of the Birdsong Shale constitutes the "bryozoan zone" (sensu Gibson, 1988) and is characterized by thin, laterally continuous beds of skeletal packstone with thin shale interbeds. This interval contains some of the best-preserved crinoid specimens, including

individuals of *Lecanocrinus meniscus* Springer and *Stiptocrinus nodosus* (Springer) with stalks and holdfasts. The bryozoan zone contains a diverse assemblage of twenty-one echinoderm species (eighteen genera) that includes the "reappearances" of some species that otherwise occur only in the more carbonate-rich strata of the Decatur Limestone and Rockhouse Limestone. For example, "*Siphonocrinus*" *dignis* Strimple occurs only in the Decatur Limestone and the bryozoan zone of the Birdsong Shale, and both *Stiptocrinus nodosus* and *Thalamocrinus ovatus* Miller and Gurley occur in the Decatur Limestone and lower Rockhouse Limestone as well as the bryozoan zone. *Lecanocrinus meniscus* and *Thalamocrinus elongatus* Springer are known from the lower Rockhouse and the bryozoan zone. *Crinobrachiatus* sp., which is found in the lower Rockhouse Limestone and bryozoan zone, is only rarely encountered in the intervening shales. Except for the last form, these species are not known from the more shaly parts of the Ross Formation, and may have been ecologically excluded from areas characterized by frequent episodic influxes of siliciclastic mud.

Overall, disparid and cladid crinoids exhibit the greatest diversity in the bryozoan zone. Altogether, there are six species of echinoderms that first appear in the bryozoan zone of the Birdsong Shale, most notably the camerates *Dolatocrinus helderbergensis* Springer and *Marsupiocrinus* (*Amarsupiocrinus*) n. sp. *Dolatocrinus helderbergensis* is the oldest known dolatocrinid and is relatively common in the bryozoan zone. Representatives of this genus are not known again until the Eifelian (Onondaga and Jeffersonville Limestones, New York, and Ohio–Kentucky). Specimens of an as-yet undescribed species of *Marsupiocrinus* (*Amarsupiocrinus*) represent the latest known occurrence of this subgenus and the first of Devonian age. "*Kooptonocrinus*" *borealis* Jell and Holloway (the holotype is a specimen originally referred to *Ampheristocrinus typus* Hall), which last appears in the Brownsport Group (Ludlovian) below the Decatur Limestone, reappears in the bryozoan zone of the Birdsong Shale. It might be noted here that G.C. McIntosh (personal commun., 1991) believes that Jell and Holloway (1983) were correct in recognizing this as a species distinct from *A. typus* Hall, but does not agree with the generic assignment.

Forty-five species found during this study have been noted only in the Decatur–Ross interval. An exception is *Marsupiocrinus tennesseensis* (Roemer), which was known previously from the Decatur Limestone and also in the underlying Brownsport Group. Additionally, eleven species (Table 2) have been described previously from the Decatur Limestone and Ross Formation, but lack precise stratigraphic data. *Eucalyptocrinites occidentalis* (Springer), *E. sculptilis* Springer, *E. sp. E* of Clement (1989), and *Cremacrinus decatur* Springer all occur in the Decatur Limestone, and apparently not elsewhere. *Scyphocrinites spinifer* Springer, *Myelodactylus schucherti* Springer, *Ichthyocrinus devonicus* Springer, *Edriocrinus dispansus* Springer, *E. explicatus* Springer, *E. occidentalis* Springer, and *Gazacrinus stellatus* Springer are reported from the undifferentiated Ross Formation (Table 3).

Stratigraphic range extensions

The Decatur Limestone and Ross Formation have an abundant and diverse echinoderm fauna. This fauna includes sixteen genera and twenty-four species that have been reported previously, and twenty-two genera and forty-five species newly reported herein. The composition of the Decatur fauna with its sixteen genera, although much greater in diversity than previously reported, is consistent with the conclusion of Sevastopulo et al. (1989) that Pridolian echinoderm assemblages are

characterized by low diversity and the presence of genera that first appear in Ludlovian or older strata (true for nine of the sixteen Decatur genera). Of the taxa in the Decatur–Ross interval, fifteen genera and nineteen species are recognized herein as having extended stratigraphic ranges. Most of these species were known previously from lower horizons. Ranges for previously described taxa were taken from Bassler and Moodey (1943), Webster (1973, 1977, 1986, 1988), and original references.

Two species, *Stiptocrinus benedicti* (Miller) and *Lecanocrinus pusillus* (Hall), now reported from the Decatur Limestone, have been known previously only from Wenlockian age rocks; *S. benedicti* occurs in the Laurel Limestone (Tennessee), and *L. pusillus* is known from the Waldron Shale (Tennessee and Indiana) and the Racine Dolomite (Wisconsin). However, the largest number (nine) of the echinoderm species reported herein from the Decatur and Ross formations were originally described from the Brownsport Group (Ludlovian, Tennessee), which underlies the Decatur Limestone. These include *Lampterocrinus tennesseensis* Roemer, *Macrostylocrinus levis* Springer, *M. pustulosus* Springer, *Marsupiocrinus excavatus* (Springer), *Pisocrinus sphaericus* Rowley, *Thalamocrinus ovatus* Miller and Gurley, “*Koootoonocrinus*” *borealis* Jell and Holloway, *Lecanocrinus pisiformis* (Roemer), and *L. meniscus* Springer. Of these species, three (*L. tennesseensis*, *M. excavatus*, *P. sphaericus*) are not found higher than the Decatur Limestone, and two species (*T. ovatus*, *L. pisiformis*) occur in both the Decatur Limestone and the Ross Formation. *Macrostylocrinus levis* and *M. pustulosus* occur only in the Rockhouse Limestone member of the Ross Formation; *L. meniscus* has been found in both the lower Rockhouse Limestone and upper Birdsong Shale (bryozoan zone); and “*K.*” *borealis* has been found only in the bryozoan zone.

Stiptocrinus nodosus Springer, which was originally reported from the Decatur Limestone (Springer, 1926), is now known from the lower Rockhouse Limestone and upper Birdsong Shale (bryozoan zone) as well. Finally, a new species of *Marsupiocrinus* (*Amarsupiocrinus*) is the first representative of this subgenus from Devonian-age rocks.

Several crinoid species from the Decatur–Ross interval have been noted only in older strata outside Tennessee. *Thalamocrinus robustus* McIntosh and Brett and representatives of the genus *Crinobrachiatus* have been previously reported only from the Rochester Shale (Wenlockian) of New York and Ontario. Both occur in the lower Rockhouse Limestone, and *Crinobrachiatus* sp. also occurs in the upper Birdsong Shale (bryozoan zone). *Hexacrinites carinatus* Strimple, which is known from the Henryhouse Formation (Ludlovian–Pridolian) of Oklahoma has been found in the Decatur Limestone and lower Rockhouse Limestone. “*Siphonocrinus*” *dignis* Strimple, another species known from the Henryhouse Formation, occurs also in the Decatur and upper Birdsong (bryozoan zone).

Finally, two taxa have been previously reported only from younger strata. *Edriocrinus pyriformis* Hall, known from the early Middle Devonian (Eifelian) Onondaga Limestone of New York, occurs in the lower Rockhouse Limestone; this represents an extension of its range downward to the Lochkovian. The occurrence of “*Kallimorphocrinus*” sp. in the Birdsong Shale apparently extends the range of this genus downward from the Mississippian.

Biogeography

Few areas have well-documented echinoderm faunas of Pridolian to Lochkovian age with which to compare the faunas of the Decatur

Limestone and Ross Formation. The best described faunas from this interval in North America are from the Henryhouse (Ludlovian to Pridolian) and Haragan (Lochkovian) Formations of Oklahoma, the Bainbridge (Ludlovian to Pridolian) and Bailey (Lochkovian) Formations of Missouri and Illinois, the Keyser Formation (Pridolian to Lochkovian) of Virginia and West Virginia, and the Coeymans Limestone and New Scotland Formation (Lochkovian) of New York. Two well-documented European faunas that are similar to that found in west-central Tennessee are those of the Armorican Massif of France and the Bohemian region of Czechoslovakia. Comparisons (Table 4) are made herein at the generic level because (1) there are slight age differences between some of the faunas, and (2) there is a strong probability that specimens would not be recognized as conspecific by paleontologists working in North America and Europe. Lower Devonian, especially Lochkovian, faunas are reported to have a high degree of endemism (Witzke et al., 1979; McIntosh and Macurda, 1981). However, this report suggests that several genera are geographically widespread (Table 4).

Similarities with coeval faunas

The Henryhouse Formation (Ludlovian–Pridolian) of Oklahoma contains abundant crinoids that were studied by Strimple (1963). It shares the greatest number of genera and species (Table 4) with the Decatur Limestone and Ross Formation, as might be expected from its geographic proximity. Strimple (1963) correlated the Henryhouse with the Decatur and listed thirty-one genera of crinoids and one blastoid. Of these, fifteen genera of crinoids and the blastoid occur in the Decatur Limestone or Ross Formation; most are known from the Decatur. Ten species are also present in both Oklahoma and Tennessee: the crinoids *Thalamocrinus elongatus* Springer, “*Siphonocrinus*” *dignis* Strimple, *Elpidocrinus tholiformis* Strimple (originally reported from the Decatur and named *Mariocrinus rotundus* by Springer [1926]—the holotype is a teratologic specimen of *E. tholiformis* Strimple [see Broadhead, 1988]), *Lampterocrinus tennesseensis* Roemer, *Hexacrinites carinatus* Strimple, *H. adaensis* Strimple, *Macrostylocrinus laevis* Springer, *Stiptocrinus benedicti* (Miller), and *Scyphocrinites elegans* Zenker and the blastoid *Polydeloideus enodatus* Reimann and Fay.

Strimple (1963) also reported six genera of crinoids from the Haragan Formation (Lochkovian) of Oklahoma; four (*Scyphocrinites*, *Edriocrinus*, *Myelodactylus*, and *Lecanocrinus*) also occur in the Ross Formation. Only one species, *Edriocrinus dispansus* Springer, is present in both formations.

Bassler and Moodey (1943) listed six genera (twelve species) from the Bainbridge Formation (Missouri and Illinois, Ludlovian–Pridolian), a correlative of the Decatur. Three genera and species (*Thalamocrinus ovatus* Miller and Gurley [see Ausich, 1987, and McIntosh and Brett, 1988, for discussion of this species], *Lecanocrinus pisiformis* (Roemer), and *Pisocrinus sphaericus* Rowley) also occur in the Decatur Limestone or Ross Formation. The Bailey Formation (Missouri and Illinois, Lochkovian), which correlates in part with the Ross Formation, also contains six described genera (seven species) (Bassler and Moodey, 1943), three of which (*Lecanocrinus* [originally *Alsopocrinus*; see McIntosh, 1981], *Edriocrinus*, and *Scyphocrinites*) also occur in the Ross Formation. Only one species, *Scyphocrinites elegans* Zenker, also occurs in Tennessee (upper Decatur Limestone).

The Coeymans Limestone (New York, Lochkovian) has eight reported genera (Bassler and Moodey, 1943), three of which (*Eudimerocrinus*, *Brachiocrinus*, and *Scyphocrinites*) occur in the Decatur Limestone and Ross Formation. One species, *Scyphocrinites*

stellatus (Hall), occurs in all three units. The New Scotland Formation (New York, Lochkovian) contains seven described genera (Bassler and Moodey, 1943), of which three (*Edriocrinus*, *Brachiocrinus*, and *Scyphocrinites*) occur in the Decatur Limestone or Ross Formation. One New Scotland species, *Edriocrinus pocilliformis* Hall, was reported from the Ross Formation (Dunbar, 1919), but taxonomic assignment of those specimens is probably incorrect (see Clement, 1989).

The Keyser Formation (Pridolian–Lochkovian; Maryland, West Virginia) contains numerous echinoderms, including many rhombiferan cystoids. However, of the fifteen genera listed by Bassler and Moodey (1943) and Springer (1926), only *Myelodactylus* and *Scyphocrinites* occur also in the Decatur Limestone or Ross Formation. *Scyphocrinites stellatus* (Hall) is the only species known in both the Keyser Formation and the Decatur–Ross interval.

As noted above, two well-described European faunas can be compared to those of the Decatur Limestone and Ross Formation of west-central Tennessee. Although no species are common to both continents, similarity at the genus level is striking. The Armorican Massif of France contains fossiliferous Lower Devonian strata (Lochkovian to Pragian) from which numerous crinoids have been reported (Le Menn, 1985, 1987). Le Menn (1985, 1987) described twenty-two genera of crinoids of Lochkovian to Pragian age (excluding those based only on stalks and columnals, except for *Myelodactylus*), of which seven also occur in the Decatur or Ross (*Dimerocrinites*, *Eohalysiocrinus*, *Pisocrinus*, *Myelodactylus*, *Theloreus*, *Lecanocrinus*, and *Stiptocrinus*). More recently, a distinctive stoloniferous holdfast originally described from

the Ross Formation (Clement et al., 1987) has been documented from Algeria (Le Menn, 1989).

Comparison of these Tennessee faunas with those of the Bohemian region of Czechoslovakia is even more striking. Prokop (1962, 1980, 1987), Breimer et al. (1968), and Macurda (1983) have reported numerous echinoderms from Pridolian through Pragian strata of Bohemia. Of the twenty-nine genera of echinoderms from those rocks, thirteen also occur in the Decatur Limestone or Ross Formation. These include ten crinoid genera (*Eucalyptocrinites*, *Scyphocrinites*, *Eohalysiocrinus*, *Pisocrinus*, *Pygmaeocrinus*, *Theloreus*, *Ichthyocrinus*, *Lecanocrinus*, *Edriocrinus*, *Hexacrinites*), two blastoid genera (*Polydeltoideus*, *Decaschisma*), and one cyclocystoid genus (*Sievertsia*) (Prokop, 1962, 1987; Breimer et al., 1968). In addition, *Ramacrinus brevis* Le Menn, which occurs in Bohemia, is a species that closely resembles *Theloreus americanus* (Springer) (Clement, n. comb.) from Tennessee; these two species are almost certainly congeneric.

An oceanic connection must have existed between these European and Tennessee echinoderm communities in Late Silurian to Early Devonian times. Reconstructions by Barrett (1985; see Figure 2A) and Morzadec et al. (1989; see Figure 2B) show this connection. The number of genera common to Bohemia and Tennessee is similar to the number common to the Henryhouse Formation (Oklahoma) and the Decatur Limestone and Ross Formation. However, many of the genera from Lochkovian rocks in Tennessee are not seen in Bohemia until the Pragian, which suggests a west to east migration route as opposed to the east to west route that Witzke et al. (1977) proposed for the migration of *Scyphocrinites*. The first interpretation is also supported by Stukalina

CRINOIDEA	Oklahoma	Missouri	New York	Maryland	Bohemia	Armorica
Cameraata						
"Siphonocrinus"	X					
Elpidocrinus	X					
Eudimerocrinus			X			
Dimerocrinites						X
Lampterocrinus	X					
Gazacrinus	X					
Stiptocrinus	X					X
Hexacrinites	X				X	
Scyphocrinites	X	X	X		X	
Eucalyptocrinites	X				X	
Macrostylocrinus	X					
Marsupiocrinus	X		X			
Disparida						
Theloreus					X	X
Eohalysiocrinus					X	X
Pisocrinus	X		X		X	X
Myelodactylus	X		X	X		X
Pygmaeocrinus					X	
Cladida						
Thalamocrinus	X	X				
Flexibilia						
Lecanocrinus	X	X			X	X
Ichthyocrinus	X				X	
Edriocrinus	X	X	X		X	
BLASTOIDEA						
Leptoschisma					X	
Polydeltoideus	X				X	
EDRIOASTEROIDEA						
Pyrgocystis			X		X	
CYCLOCYSTOIDEA						
Sievertsia					X	

Table 4. Echinoderm genera common to the Decatur and Ross formations of Tennessee and to other areas with relatively well-documented and diverse echinoderm faunas of Late Silurian and Early Devonian age.

(1977), who indicated only Lower Devonian occurrences of *S. stellatus-mutabilis* in Europe, and Upper Silurian occurrences elsewhere. Oceanic currents, as reconstructed by Barrett (1985; see Figure 2A), support this view.

Geographic range extension

Eleven species of echinoderms reported herein occur in Tennessee and elsewhere in Pridolian to Pragian (Siegenian) age strata. Five species have been reported earlier from the Henryhouse Formation of Oklahoma (Strimple, 1963; Breimer and Macurda, 1972): "*Siphonocrinus*" *dignis* Strimple, *Elpidocrinus tholiiformis* Strimple, *Hexacrinites carinatus* Strimple, *H. adaensis* Strimple, and *Polydeltoideus enodatus* Reimann and Fay.

Scyphocrinites elegans Zenker, a species common in Pridolian through lower Lochkovian strata of Bohemia, is also found in the Bailey Limestone (Lochkovian) of Missouri, and has now been recovered from the Decatur Limestone (Pridolian). The disparid genus *Eohalsiocrinus*, noted in Wenlockian rocks of Bohemia (Prokop, 1987), occurs in Lochkovian rocks (Ross Formation) of Tennessee. *Theloreus*, a characteristic Armorican genus (Lochkovian to Pragian; Le Menn, 1985), is recognized herein for the first time in North America with the reassignment of *Phimocrinus americanus* Springer to *Theloreus* (Clement, n. comb.). *Pygmaeocrinus*, until now known only from Lower Devonian rocks of Bohemia (Strimple, 1963; Prokop, 1987), has been found in the upper Birdsong Shale (uppermost brachiopod zone) of Lochkovian age. Specimens of *Sievertsia* sp., a genus originally reported from Bohemia, occur throughout the upper Rockhouse Limestone to upper Birdsong Shale (bryozoan zone) interval, and represent the first report of cyclocystoid remains from Lochkovian-age rocks. The occurrence of the edrioasteroid *Pyrgocystis* sp. marks the first report of a member of this genus from west-central Tennessee.

As mentioned above in the discussion of biostratigraphy, *Thalamocrinus robustus* and *Crinobrachiatus* sp. have been reported only from the Rochester Shale (Wenlockian) of western New York State and southern Ontario, but are now known to occur in the lower Rockhouse Limestone. This report extends their range geographically as well as stratigraphically. Similarly, specimens referred to *Edriocrinus pyriformis* Hall, a species known from New York (Eifelian, Onondaga Limestone), occur in the older strata of the Ross Formation.

Implications for dispersal mechanisms and patterns

The only previous comprehensive discussion of Silurian and Early Devonian echinoderm biogeography has been provided by Witzke et al. (1979). That report attempted to analyze cosmopolitan and endemic distributions, principally at the family level. Witzke et al. (1979) noted an apparent decrease in the areal extent of carbonate platforms from the Wenlockian to the end of the Silurian, which they believed to be important in contributing to a decline in taxonomic diversity. This report and the unpublished data of Clement (1989) supplement some of the conclusions of Witzke et al. (1979). Documentation of thirty-one species from the Decatur Limestone contrasts significantly with the nine species earlier reported by Springer (1926) and used by Witzke et al. (1979) in their synthesis. The occurrence of these species in carbonate platform deposits appears to strengthen the conclusion that carbonate platforms provided near-optimum conditions for diverse echinoderm assemblages.

Patterns of paleogeographic distribution may yield inferences concerning larval development, even when skeletonized evidence is

lacking. Planktotrophic and lecithotrophic larvae are well-documented in modern echinoids and gastropods; both groups include species with morphologic features that are useful indicators of these types of larval development. Witzke et al. (1979) specifically discussed the widespread distribution of the cladid crinoid *Petalocrinus* and the camerate *Scyphocrinites*. Whereas the bulbous, chambered root termination of *Scyphocrinites* has been interpreted as a flotation structure (Haude, 1972) that provided dispersal potential in the adult stage, sessile crinoids, including *Petalocrinus* and most taxa considered herein, would have relied entirely upon dispersal in the larval stage.

Distributional comparisons presented herein (Table 4) do not consider the earlier biogeographic histories of key taxa. Nonetheless, comparison of patterns may reflect real biologic differences, even at higher taxonomic levels, that may have influenced dispersal. More detailed field studies of key areas and regional syntheses are necessary to answer some of the questions posed herein.

Did camerate crinoids have limited larval dispersal? The close biogeographic tie to the Hunton Group of Oklahoma is heavily supported by similarities in genera and species of camerate crinoids, whereas few camerate genera occur in other well-documented areas. The possible adult dispersal of *Scyphocrinites* has been mentioned above, and the small number of other camerates that occur elsewhere are mostly genera (e.g., *Eucalyptocrinites*) with more widespread distributions earlier in the Silurian.

Did disparid and flexible crinoids tend to have wide larval dispersal? Disparids are commonly characterized by small dorsal cups or characteristic stem morphologies (Myelodactylidae) that facilitate their collection and recognition. *Pisocrinus* has a distinctive cup, which is commonly found articulated, and its apparent widespread occurrence, along with that of myelodactyliids, may be an artifact of taphonomy and ease of recognition. Considerably more argillaceous strata must be disaggregated to provide data relevant to detailed distributional analysis of small disparids. The flexibilia, on the other hand, include a mixture of widespread genera and those with limited geographic distribution, and no clear pattern emerges.

In addition to the crinoids, a small number of other echinoderms (e.g., *Leptoschisma*, *Polydeltoideus*, *Pyrgocystis*, *Sievertsia*) (Table 4) exhibit an indication of widespread dispersal. Overall, however, the biogeographic patterns shown here are still wholly inadequate to provide anything but a broad general comment about migration routes and larval development of Silurian and Devonian echinoderm faunas.

Acknowledgments

The authors thank Appalachian Basin Industrial Associates and the Discretionary Funds of the Department of Geological Sciences, The University of Tennessee, for funding. M.A. Gibson, University of Tennessee, Martin, was of great assistance in the field and provided shale samples for disaggregation. We also thank T.E. Guensburg, Southern Illinois University at Edwardsville, for contributing specimens. The generosity of Vulcan Materials Corporation in permitting access to its operating quarries in the study area of west-central Tennessee was essential to the completion of this study. We are particularly indebted to G.C. McIntosh for suggestions concerning taxonomic affinity and distributions of key taxa, and to W.I. Ausich and E. Landing for valuable critiques of this manuscript. The University of Tennessee supplied \$200 toward publication of this report.

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Calmoniid trilobites from the Devonian Fox Bay Formation, Falkland Islands: Systematics and biogeography

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Abstract

Calmoniidae from the Emsian Fox Bay Formation include *Bainella* Rennie, *Metacryphaeus* Reed, and *Oosthuizenella* Cooper. Each genus is represented by a species also known from the South African Bokkeveld Group or is most closely related to a Bokkeveld species. "*Dalmanites*" *falklandicus* Clarke is a distinct species of *Bainella*; *Bainella nilesi* n. sp. is a sister species to *B. africana* (Salter). Fox Bay *Oosthuizenella ocellus* (Lake) is indistinguishable from South African specimens, and *Metacryphaeus allardyceae* (Clarke) is subtly differentiated from *M. caffer* (Salter). Hypostomes are described for *Bainella*, *Oosthuizenella* (sister genus to *Pennaia* Clarke), and *Deltacephalaspis*. Occurrences are confirmed for Andean *Calmonia* Clarke (in the *Scaphiocoelia* Zone, Bolivia), and Brazilian *Kozlowskiaspis* Braniša and Vaněk (*K. subseciva* [Clarke], from the Ponta Grossa Formation, Paraná). Area relationships derived from calmoniid species' cladograms predict two informative resolutions for the affinities of the South African fauna; it has its most recent history with the Falklands or with the Paraná Basin and Andean shelf.

Introduction

J. M. Clarke's (1913a) monograph has remained the sole taxonomic work on trilobites from the Emsian Fox Bay Formation, West Falkland Island. Four species were assigned to the Family Calmoniidae: *Cryphaeus?* *allardyceae* Clarke, 1913; *Dalmanites falklandicus* Clarke, 1913; *D. (Mesembria) acacia* Schwarz, 1906; and *Calmonia ocellus* Lake, 1904. This report features a taxonomic revision of calmoniid species in this fauna (see Figure 1 for localities) in light of extensive changes in the group's classification since Clarke's study (Struve, 1959; Eldredge and Braniša, 1980; Cooper, 1982).

The Fox Bay Formation consists of 760–800 m of fossiliferous shale and thin- to medium-bedded micaceous quartzitic sandstone (Mitchell-Thome, 1970). The Formation conformably overlies the Early Devonian Port Stephens Formation, and lies below the Middle–Late Devonian Monte Maria Formation (Barrett and Isaacson, 1988). The abundant trilobite fauna at Pebble Island is typically preserved in pyritic, dark grey siltstone nodules. An Emsian age assignment for the Fox Bay Formation has been based on its Malvinokaffric trilobite and brachiopod faunas. Revision of the calmoniid trilobites herein confirms a late Emsian age that indicates correlation with the Gydo Shale of the Bokkeveld Group in South Africa (Cooper, 1982, 1986). Evidence for

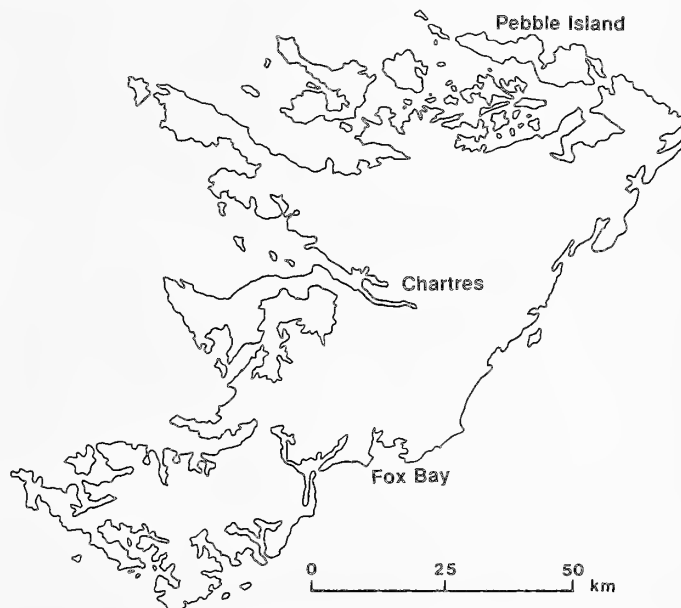


Figure 1. Map of West Falkland Island, showing general locations of calmoniid collections at Chartres River, Fox Bay, and Pebble Island.

this correlation includes the common presence of *Oosthuizenella ocellus* (Lake) and closely related species of *Bainella*.

The morphological terminology of this report is generally that used by Eldredge and Braniša (1980). Glabellar lobes and furrows are numbered as by Jaanusson (1956), with the prefix L or S, respectively, and suffix 0 (occipital) to 4 (anterior). "Large Eye Index" is measured by Wolfart's (1968) criteria, as is the ratio of the maximum exsagittal length of the eye to the sagittal length of the glabella (excluding S0).

The specimens figured or cited in this work are housed in the following collections: Department of Invertebrates, American Museum of Natural History (AMNH), New York City; Department of Palaeontology, British Museum (Natural History) (BM IN), London; Departamento Nacional da Produção Mineral (DGM), Rio de Janeiro; and New York State Museum (NYSM), Albany.

Family CALMONIIDAE Delo, 1935

Subfamily CALMONIINAE Delo, 1935

Genus OOSTHUIZENELLA Cooper, 1982

Type species.—*Phacops ocellus* Lake, 1904, by original designation.

Discussion.—*Oosthuizenella* is a monotypic genus that is based on a geographically widespread type species that occurs in South Africa and the Falkland Islands (see below). Cooper (1982) compared *Oosthuizenella* to *Calmonia* Clarke, 1913, and *Pennaia* Clarke, 1913. His proposed classification (Cooper, 1982, p. 63) assigned it to a *Phacopina* plexus (with the eponymous genus, *Pennaia*, and *Andinacaste* Eldredge and Braniša, 1980), rather than the *Calmonia* plexus. These groupings were not diagnosed; the *Phacopina* plexus (because it includes the acastomorph *Andinacaste*) is certainly based on symplesiomorphy. The hypostome of *Oosthuizenella ocellus*, described below, reveals some distinctive derived characters shared with that of

Pennaia from the Belén and Sicasica Formations of Bolivia (Plate 1, figure H; see Wolfart, 1968, Pl. 22, figs. 6, 7). *Pennaia* from Bolivia has traditionally been assigned to *Acastoides* Delo, 1935 (Subfamily Acastinae). Eldredge and Braniša (1980) provided evidence that Malvinokaffric "*Acastoides*" are Calmoniinae that are convergent on Silurian–Devonian Boreal *Acastoides*. Cooper (1982) supported this view and referred these species to *Pennaia* Clarke, 1913. In hypostomes of *Oosthuizenella ocellus* and Bolivian *Pennaia*, the maculae are positioned closer to the anterior margin of the middle body than in other calmoniines, and are also spaced more closely to each other. The round outline of the middle body, short borders, and absence of marginal

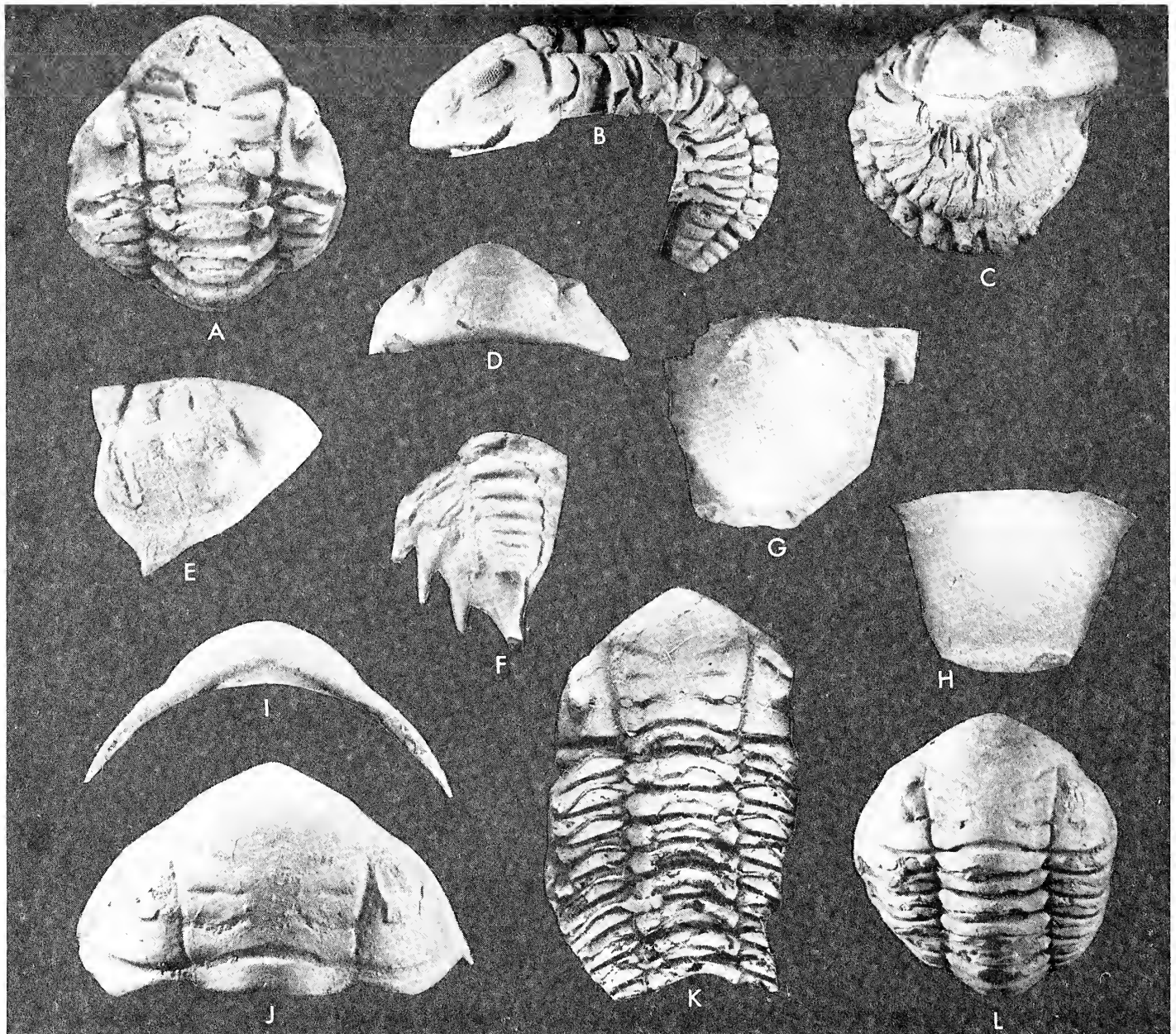


Plate 1. A-G, I-L, *Oosthuizenella ocellus* (Lake, 1904). Fox Bay Formation, Pebble Island, West Falkland. A, C, dorsal cephalic and lateral views of enrolled exoskeleton, internal mold, hypotype NYSM 9647, x2; B, D, L, lateral, anterior, and dorsal cephalic views of partly enrolled exoskeleton, internal mold, hypotype NYSM 9646, x2; E, I, J, lateral, ventral, and dorsal views of cephalon, hypotype NYSM 16119, x3; F, dorsal view of pygidium, internal mold with traces of cuticle, hypotype NYSM 16120, x3; G, ventral view of hypostome, hypotype NYSM 9646, x6; K, dorsal view of cephalon and anterior eight segments of thorax, internal mold, hypotype NYSM 16121, x3; H, *Pennaia* sp. Belén Formation, undetermined locality, La Paz Department, Bolivia. Ventral view of hypostome, latex cast from external mold, hypotype AMNH 44155, x6.

spines are also similar. The hypostome of *Kozlowskiaspis subseciva* (Clarke, 1913a, Pl. 7, fig. 3; 1913b, Pl. 10, fig. 2) differs in its longitudinally ovate middle body and laterally positioned, well-separated maculae (see below for reassignment of this species from *Calmonia*). The hypostomal characters of *Calmonia* Clarke are unknown. These unique similarities in hypostomal morphology support Cooper's (1982) contention that *Oosthuizenella* and *Pennaia* are closest relatives, a relationship that is suggested on the basis of other character systems. This provides additional evidence that supposed Malvinokaffric "*Acastoides*" are Calmoniinae rather than Acastinae.

If *Phacops ocellus* Lake is assigned to *Oosthuizenella*, the genus *Calmonia* is not known to occur in the Falklands. This species formed the basis for the geographic distribution data of Baldis (1979) and Eldredge and Ormiston (1979). Undoubted occurrences of *Calmonia* are restricted to the type species in Paraná (Clarke, 1913a) and Arroyo del Cordobes, Uruguay (along with several possible junior synonyms or closely related species of Mendez-Alzola [1938]).

Although retained in *Calmonia* in recent works (e.g., Carvalho et al., 1987), *Calmonia subseciva* Clarke, 1913, differs from typical *Calmonia* in the form of its genal angle and absence of a pygidial posteromedian spine. Diagnostic features of *Kozlowskiaspis* Braniša and Vaněk, 1973, that are shared with the latter species include the following: a wide, diamond-shaped frontal glabellar lobe; broadly shouldered cephalic outline; broadly arched cephalic anterior border process; thoracic pleurae terminating as sharp, posteriorly directed spines; and pygidial axis extending nearly to the posterior margin (Plate 2). *Kozlowskiaspis subseciva* from Paraná is very similar to Bolivian *K. superna* Braniša and Vaněk, 1973. This generic reassignment provides the first record of

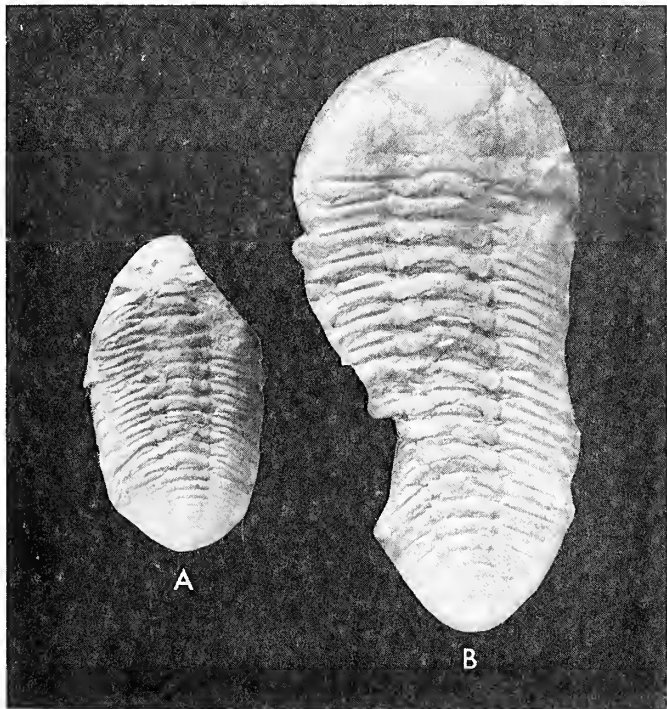


Plate 2. *Kozlowskiaspis (Kozlowskiaspis) subseciva* (Clarke, 1913). Jaguariáiva Member, Ponta Grossa Formation, Jaguariáiva, Paraná, Brazil. A, dorsal view of exoskeleton, internal mold, paralectotype DGM 28-1 (original of Clarke, 1913a, Pl. 7, fig. 6), x1.5; B, dorsal view of exoskeleton, internal mold, lectotype (designated herein) DGM 25-1 (original of Clarke, 1913a, Pl. 7, fig. 9), x1.5. Photos courtesy of M. da G.P. de Carvalho (Rio de Janeiro).

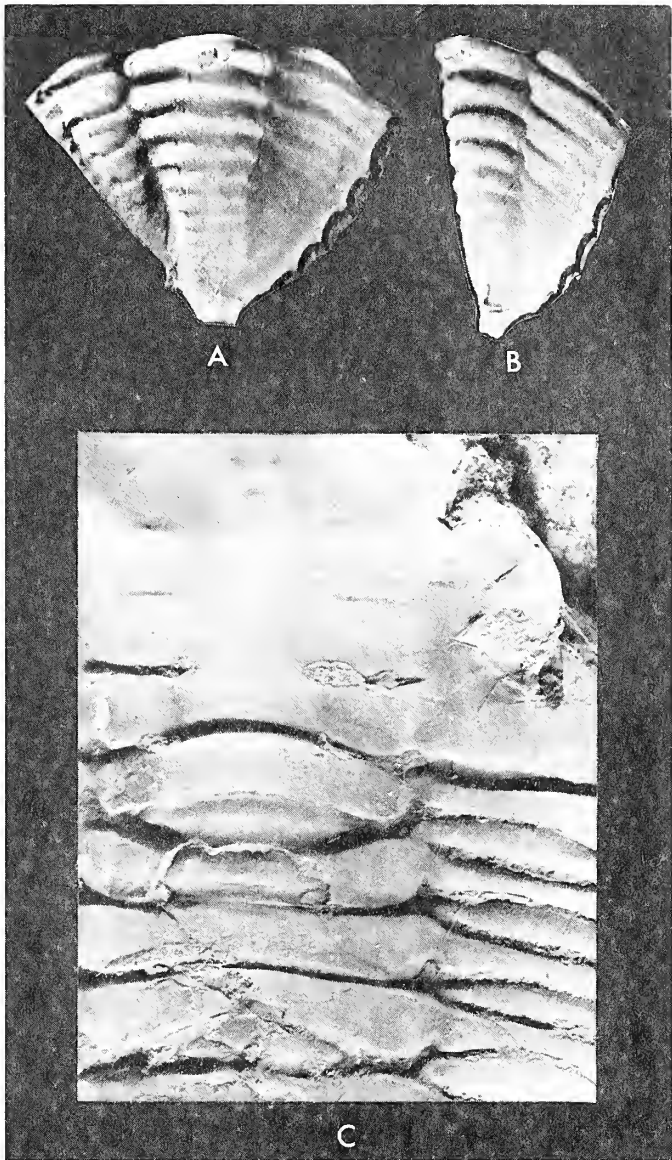


Plate 3. A, B, *Calmonia* sp. Gamonedá Formation, Scaphiocoelia Zone, Curuyo, Tarija Department, Bolivia. Dorsal and lateral views of pygidium, internal mold, hypotype AMNH 44159, x3; C, *Calmonia signifer* (Clarke, 1913), Jaguariáiva Member, Ponta Grossa Formation, Ponta Grossa, Paraná, Brazil. Dorsal view, detail of cephalon and anterior part of thorax, showing coarsely granulate prosopon on internal mold, hypotype NYSM 16122, x3.

Kozlowskiaspis in Brazil. The genus is otherwise known from Bolivia (Eldredge and Braniša, 1980) and, questionably, from South Africa (*K. ? ceres* [Schwarz]; see Cooper, 1982). A possible occurrence of the genus from Jujuy Province, Argentina, is indicated by *Australops australis* Baldis, 1972. This monotypic genus appears to nest within the cladistic structure of *Kozlowskiaspis* and is most closely related to *K. borealis* Eldredge and Braniša, 1980. Apomorphic features shared by *Australops* and *K. borealis* include a relatively large eye, a strong palpebral furrow, and free-pointed tips of the thoracic pleurae. More general diagnostic characters of *Kozlowskiaspis* that are also possessed by *Australops australis* include a broadly rounded cephalic anterior border process and a diamond-shaped frontal glabellar lobe with strong transection near the anterior branch of the facial suture (Baldis, 1972, Pl. 1, fig. 3). The pos-

sible synonymy of *Kozlowskiaspis* Braniša and Vaněk, 1973, with *Australops* Baldi, 1972, requires further study of the Argentine species.

Earlier Andean records of *Calmonia* are rejected in this report. *Calmonia curvioculata* Wolfart, 1968, is better placed in *Metacryphaeus* Reed, and species similar to *Calmonia* (Eldredge and Braniša, 1980, Fig. 29A) are doubtful representatives of the genus. However, a pygidium from the *Scaphiocoelia* Zone of the Gamoneda Formation at Curuyo, Tarija Department, Bolivia (Plate 3, figures A, B), can be assigned to *Calmonia*. It closely resembles *C. signifer* in the presence of six pairs of pygidial marginal denticles and a large postero-medial spine. Pleural furrows are distinct on the anterior five ribs (the last being very shallow). Ten complete axial rings are defined, and the coarse granules on the rings are comparable to the granulation observed on the glabella and thoracic axial rings of *C. signifer* from the Ponta Grossa Formation, Paraná (Plate 3, figure C). The *Scaphiocoelia* Zone species confirms the occurrence of *Calmonia* in Andean strata and is older than congeneric species in the Uruguayan Rincón de Alonzo and Brazilian Ponta Grossa shale.

OOSTHUIZENELLA OCELLUS (Lake, 1904)

Plate 1, figures A-G, I-L

Phacops ocellus LAKE, 1904, p. 207, Pl. 24, figs. 9, 10.

Oosthuizenella ocellus (Lake). COOPER, 1982, p. 65, figs. 45-49, 50C, 85C (with complete synonymy).

Calmonia ocellus (Lake). CLARKE, 1913a, p. 129, Pl. 5, figs. 11-15; 1913b, Pl. 7, figs. 3-7 (in part).

Material.—NYSM 9646 (Clarke, 1913a, Pl. 5, figs. 11, 12); NYSM 9647 (Clarke, 1913a, Pl. 5, figs. 13-15); figured specimens NYSM 16119-16121. NYSM 16140, internal mold of cephalon; NYSM 16141, counterpart molds of partial thorax; NYSM 16142-16144, three counterpart molds of partial articulated exoskeletons; NYSM 16145, internal mold of partial cephalon; NYSM 16146, internal mold of thoracopygidium; NYSM 16147, cephalon. Fox Bay Formation, Pebble Island, West Falkland Island.

Description of hypostome.—Hypostome small, 53% length of glabella, slightly longer than width at midlength, lateral margins gently converge backward. Anterior margin faintly convex forward (sag.), weakly concave at anterior wings. Middle body approximately circular in outline; moderately, evenly convex (sag., tr.) with pervasive, low muscle impression scars. Middle furrow obsolete; maculae prominent, ovate, close together adaxially, located immediately behind anterior margin of middle body. Anterior and lateral border furrows poorly defined (by change of slope, most gradual at anterior wing). Border narrow laterally, moderately long posterolaterally; posterolateral/posterior border furrow shallow but distinct.

Discussion.—A full description of *Oosthuizenella ocellus* (Lake) based on Gydo Formation material from South Africa has been given by Cooper (1982). To avoid redundancy, only the previously undescribed hypostome is given a full description on the basis of conspecific material from the Fox Bay Formation. No consistent differences serve to distinguish the West Falkland Island specimens from those in South African collections. As the specimens illustrated by Cooper (1982), *O. ocellus* from West Falkland Island is rather variable in width of the cephalon and shape of the frontal glabellar lobe (with length ranging from 45% to 65% of its width). Most Fox Bay specimens have relatively large eyes (Large Eye Index 0.36-0.38). However, other specimens extend into the range of variation shown by South African forms (e.g., as low as 0.29). The number of dorsoventral lens files in the visual surface ranges from twenty-three to twenty-seven (i.e., twenty-three to

twenty-four) in Gydo Formation material). Falkland *Oosthuizenella* have the anterior margin of SO less strongly arched forward sagittally than in many South African specimens. This results in SO having a more nearly constant length (sag. versus exsag.). However, this feature is variable in *O. ocellus*, and the difference is slight.

Similarly, no evidence exists to distinguish Pebble Island pygidia from those of *Oosthuizenella ocellus* from the Bokkeveld Group. Clarke (1913a, p. 130, Pl. 5, fig. 15) reconstructed at least five pairs of marginal spines and cited six "pointed lappets" in his description (versus only four pairs in Cooper's [1982] reconstruction of *O. ocellus*). NYSM 9647 (Plate 1, figure C) illustrated by Clarke, however, has only four large marginal spines preserved. A fifth pair of pleurae is present, but their terminae are broken, and evidence for the presence of free spines is equivocal. This region is not clearly preserved in any pygidia from the Gydo Formation that were figured by Cooper (1982). Evidence for the posteromedial spine seen in Gydo pygidia, as well as only four pairs of marginal spines, is provided by a well-preserved Pebble Island pygidium (Plate 1, figure F). Three marginal spines are observed anterolateral to the posteromedial spine; the anteriormost is associated with the second of eight axial rings, and it is inferred that a first pair of marginal spines was also present (i.e., four in total).

Genus BAINELLA Rennie, 1930

Type species.—*Bainella bokkeveldensis* Rennie, 1930 (= *B. africana* [Salter, 1856] fide Cooper [1982]), by original designation.

Discussion.—Eldredge and Braniša (1980) recognized two subgenera within *Bainella*. These include the eponymous subgenus and *Belenops* Eldredge and Braniša, 1980. Cooper (1982, p. 127) rejected the subgeneric status of *Belenops* and cited problems in the group's relationships if pygidial characters are considered. Nonetheless, he endorsed the view that species referred to *Belenops* by Eldredge and Braniša (i.e., *B. insolita* (Wolfart, 1968) and *B. gamkaensis* Rennie, 1930) are each other's closest relatives, and indeed proposed a direct ancestor-descendant relationship. As such, Cooper's interpretation of *Belenops* would have a reasonable basis only if it can be demonstrated that recognition of this (monophyletic) subgenus renders *B. (Bainella)* a paraphyletic group (i.e., united solely by plesiomorphy).

Ontogenetic transformations of *Bainella (Belenops) insolita* provide evidence that some of the characters used by Eldredge and Braniša (1980) to diagnose *B. (Bainella)* are primitive relative to the condition in *B. (Belenops)*. Cephalon from the *Scaphiocoelia* Zone at Curuyo, Tarija Department, Bolivia, are inferred to be juveniles (small holaspides?) of *B. (Belenops) insolita*; the latter species is, indeed, known from

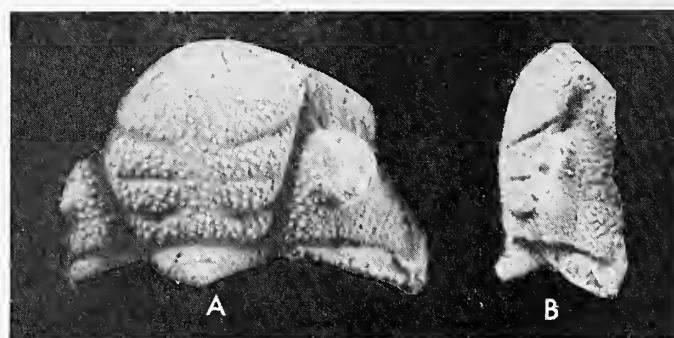


Plate 4. A, B, *Bainella insolita* (Wolfart, 1968). Gamoneda Formation, *Scaphiocoelia* Zone, Curuyo, Tarija Department, Bolivia. Dorsal and lateral views of cephalon, latex cast from external mold, hypotype AMNH 44156, x5.

Table 1. Characters and character state matrix used to construct cladogram in Figure 1. Plesiomorphic state is '0', except for character 11, which is coded as of undetermined state ('?') because of ambiguous outgroup codings.

- 1. anterior margin of cephalon: 0—straight anterolaterally, pointed medially; 1—rounded;
- 2. cephalic arching (tr.) / inflation of frontal glabellar lobe: 0—moderate; 1—strong;
- 3. cephalic axial furrow: 0—nearly straight; 1—sinuous, curved against L3;
- 4. cephalic tuberculation: 0—absent; 1—subdued, distinct; 2—coarse;
- 5. S3: 0—approximately straight; 1—sinuous;
- 6. S1: 0—distinctly confluent with axial furrow; 1—weakly confluent with axial furrow;
- 7. genal spine: 0—straight; 1—weakly curved inward distally; 2—prominently curved inward distally;
- 8. transverse rows of thoracopygidial axial and pleural spines: 0—absent; 1—present;
- 9. pygidial axial nodes: 0—absent; 1—present;
- 10. pygidial marginal denticles: 0—absent; 1—present;
- 11. pygidial terminus: 0—rounded; 1—terminal spine.

	1	2	3	4	5	6	7	8	9	10	11
<i>africana</i>	0	0	0	0	0	1	2	0	0	0	0
<i>nilesi</i>	0	0	0	0	0	1	1	0	0	0	1
<i>sanjuanina</i>	0	0	0	1	1	0	?	?	?	?	?
<i>arbuteus</i>	0	0	0	2	1	0	?	1	1	1	1
<i>cristagalli</i>	0	0	0	2	1	1	0	1	1	0	1
<i>insolita</i>	1	1	1	1	1	0	0	0	1	1	1
<i>gaakaensis</i>	1	1	1	0	1	0	0	0	1	0	0

this horizon and locality. The smallest specimen (Plate 4) has a glabellar length less than one-half of that of the smallest cephalon of this species as illustrated by Eldredge and Braniša (1980, Fig. 8A-D) from Curuyo. Because such small size is peculiar for species of *Bainella*, and because a somewhat larger specimen has a morphology intermediate between the smaller cephalon and that figured by Eldredge and Braniša, it seems most plausible that they represent juvenile stages of *B. (Belenops) insolita* rather than a new species.

The ontogeny of *Belenops* indicates the following transformations:

- 1. The cephalic axial furrow is nearly straight in juveniles, and becomes sinuous and constricted at L3 with growth.
- 2. S3 is nearly straight and only gently flexed at midwidth (tr.) in small cephalo. It becomes more sinuous with distinctly differentiated proximal and distal moieties with growth.
- 3. S2 and S3 are moderately incised in juveniles, and become shallower during ontogeny.
- 4. Cephalic tuberculation is pervasive in small cephalo, and equal-sized small tubercles occur on the glabella, L0, genae, borders and palpebral lobe. These are subdued in later growth stages with devel-

- opment of weak, coarse tubercles on the glabella.
- 5. Increased transverse arching of the glabella occurs with growth.
- 6. The anterior edge of the palpebral lobe is adjacent to the axial furrow in juveniles, but becomes adaxially displaced onto the gena and connected to the axial furrow by an ocular ridge in large specimens.
- 7. Decreased distinctness of the palpebral furrow develops with growth.

Transformations 1, 2, and 5 each involve a condition typical of *Bainella* (*Bainella*) and give rise to the diagnostic character state of *Belenops*. As such, straight axial furrows and S3 and weak cephalic arching are more generalized conditions in ontogeny, and are interpreted as plesiomorphic homologues (Weston, 1988). Their value in the diagnosis of *B. (Bainella)* is therefore rejected. Similarly, the anterior branch of the facial suture runs entirely outside the frontal glabellar lobe in the smallest cephalon of *B. (Belenops) insolita*. Ontogeny indicates that absence of a transection of the anterolateral portion of the frontal lobe (the *Bainella* condition) is more general than presence of a transection (the *Belenops* condition). Juveniles of *B. (Belenops) insolita* more closely approach the *B. (Bainella)* condition with straight cephalic anterolateral margins than do rounded-margined large holaspides. This evidence implies that few of the "diagnostic" characters of *B. (Bainella)* can be regarded as synapomorphies.

Table 1 summarizes the distributions of various characters that have been compared between the systematic subdivisions of *Bainella*. These data were analyzed with the parsimony program termed "Hennig86" (Farris, 1988). Polarities were determined with reference to the ontogeny of *B. insolita* where information was available (characters 1, 2, 3, and 5). Outgroup comparison was used to polarize other characters. Cooper's (1982, p. 63) contention that *Bainella* is part of a clade that

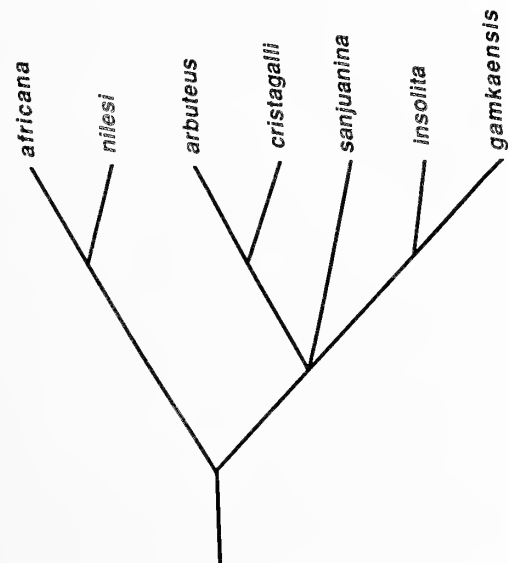


Figure 2. Strict consensus of three minimum-length cladograms (17 steps; consistency index 0.76) for *Bainella* species differentiated by Hennig86 analysis of characters in Table 1. Cladograms constructed with implicit enumeration (ie*), with multistate characters 4 and 7 additive.

includes *Kozlowskiaspis* Braniša and Vaněk and *Deltacephalaspis* Eldredge and Braniša suggests that these genera are plausible outgroups. Three minimum length cladograms (consistency index 0.76) allow the consensus shown in Figure 2.

These characters offer support for the monophyly of *Belenops* (*insolita* + *gamkaensis*) as proposed by Eldredge and Braniša (1980). The subgenus *Bainella*, if it is to be maintained as a monophyletic group, should be restricted to the sister species *B. africana* and *B. nilesi* n. sp. Synapomorphic characters include (at least weak) distal curvature of the genal spine and an S1 that is weakly confluent with the cephalic axial furrow. However, ingroup species not considered by Eldredge and Braniša (the clade *B. arbuteus* (Lake, 1904) + *B. cristagalli* (Woodward, 1873)), as well as *B. sanjuanina* Baldis, 1967, are resolved to be more closely related to *Belenops* than to *B. (Bainella)*. Rather than broadening the diagnosis of *Belenops* to accommodate these species, Cooper's (1982) assignment of all of these species to a monophyletic genus *Bainella*, without subgenera, is followed in this report.

Remarks.—Cooper (1982, pp. 129-130, fig. 57A) described and illustrated the first known *Bainella* hypostome, an internal mold from *B. africana* (Salter). A second hypostomal mold has been discovered in situ in a complete specimen of *B. africana* that was collected by N. Eldredge from the Gydo Formation at Klarstroom (Plate 5, figures C, D). Certain differences from Cooper's (1982, fig. 57A) figured specimen reveal a moderate degree of intraspecific variation. Notably, the middle body is longer (ovate rather than circular), and the hypostomal length is inferred to be almost 80% of its width. In addition, the middle furrow is poorly defined. The middle body is of moderate convexity in the sagittal plane; it is most strongly vaulted transversely near midlength. The anterior margin of the hypostome is only faintly convex forward (sag.) and has large anterior wings located along the margin; the steeply inclined wings are narrower than in Cooper's specimen. Small but distinct maculae occur far abaxially, well behind the anterior wing; their midlength is at about 40% the length of the anterior border and middle body. The *Bainella* hypostome is noteworthy for its very

weakly incised posterior border furrow; the posterolateral/posterior border is very short (and apparently aspinose), of even length (sag., exsag.), and faintly separated from the posterior lobe of the middle body by a decrease in slope.

BAINELLA FALKLANDICUS (Clarke, 1913)

Plate 6

Dalmanites falklandicus CLARKE, 1913a, p. 105, Pl. 5, figs. 3, 4; CLARKE, 1913b, Pl. 4, fig. 6 (in part).

Bainella falklandicus (Clarke). ELDREDGE AND ORMISTON, 1979, p. 167.

Metacryphaeus falklandicus (Clarke). COOPER, 1982, p. 167.

Lectotype.—Internal mold of thoracopygidium NYSM 9722 (selected herein; see Clarke, 1913a, Pl. 5, fig. 4; 1913b, Pl. 4, fig. 6). Paralectotype is counterpart mold of pygidium NYSM 9721 (see Clarke, 1913a, Pl. 5, fig. 3). Fox Bay Formation, Fox Bay, West Falkland.

Discussion.—Clarke (1913a) defined *Dalmanites falklandicus* on the basis of co-occurring specimens with similar size. It is now apparent that two species are represented by the syntypes. One syntype cephalon (Plate 7, figures D, G) belongs to *Metacryphaeus allardyceae* (Clarke), and the thoracopygidia represent a distinct species of *Bainella*. The more complete of Clarke's figured *Bainella* specimens is designated herein as a lectotype to accommodate both species without requiring a new name.

Clarke (1913a, p. 118) recognized that the pygidium of *Bainella* "acacia" (= *B. nilesi* n. sp.) resembles that of *B. falklandicus*, but suggested that the former has "a more extended caudal spine." This distinction is confirmed; the terminal spine of *B. nilesi* is elongate and curved dorsally, whereas *B. falklandicus* has a short, bluntly rounded postaxial region. The axial terminus of both *B. falklandicus* specimens is more prominent than that in pygidia of *B. nilesi*. The two species are also readily distinguished by the absence of thoracic axial spines in *B. falklandicus*. The sagittal region of all but the fifth thoracic segment of the

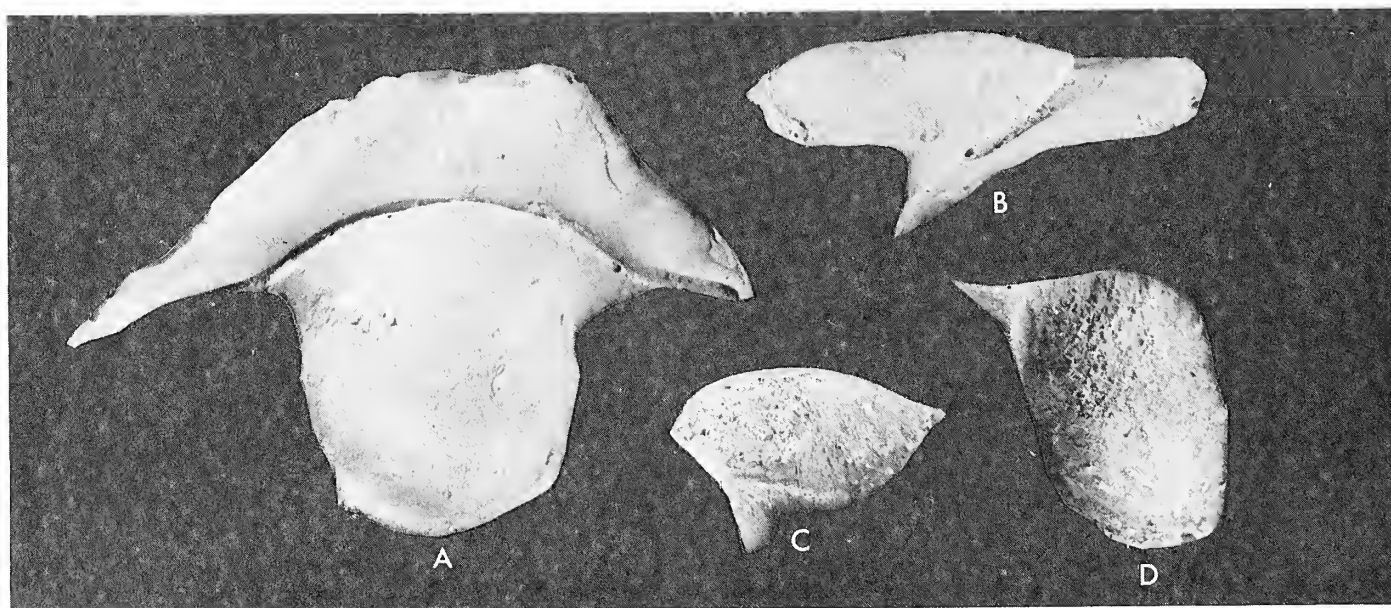


Plate 5. A, B, *Deltacephalaspis magister* Eldredge and Braniša, 1980. Belén Formation, Scaphiocoelia Zone, Colchani, La Paz Department, Bolivia. A, B, ventral and lateral views of cephalic doublure and hypostome, latex cast from external mold, hypotype AMNH 44158, x3. C, D, *Bainella africana* (Salter, 1856). Gydo Formation, Klarstroom, Cape Province, South Africa. Lateral and ventral views of hypostome, latex cast from external mold, hypotype AMNH 44157, x3.

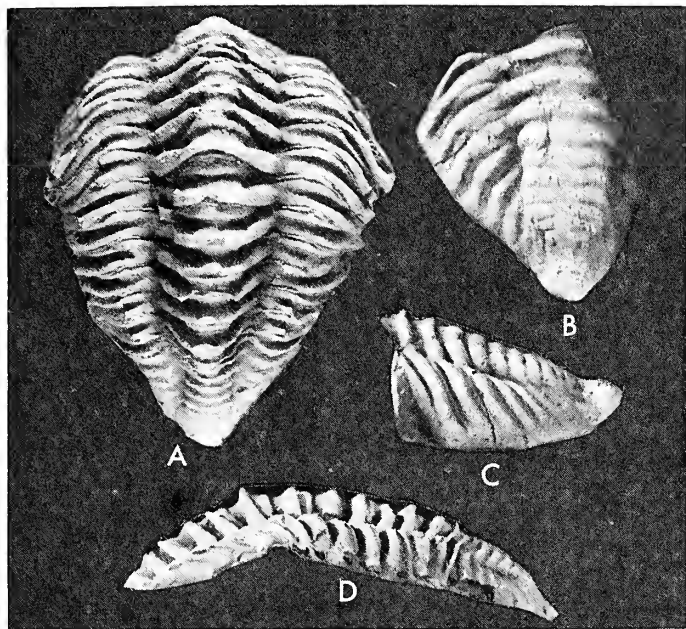


Plate 6. A-D, *Bainella falklandicus* (Clarke, 1913). Fox Bay Formation, Fox Bay, West Falkland. A, D, dorsal and lateral views of thoracopygidium, internal mold, lectotype NYSM 9722, $\times 1.5$; B, C, dorsal and lateral views of pygidium, plastic cast from external mold, paralectotype NYSM 9721, $\times 1.5$.

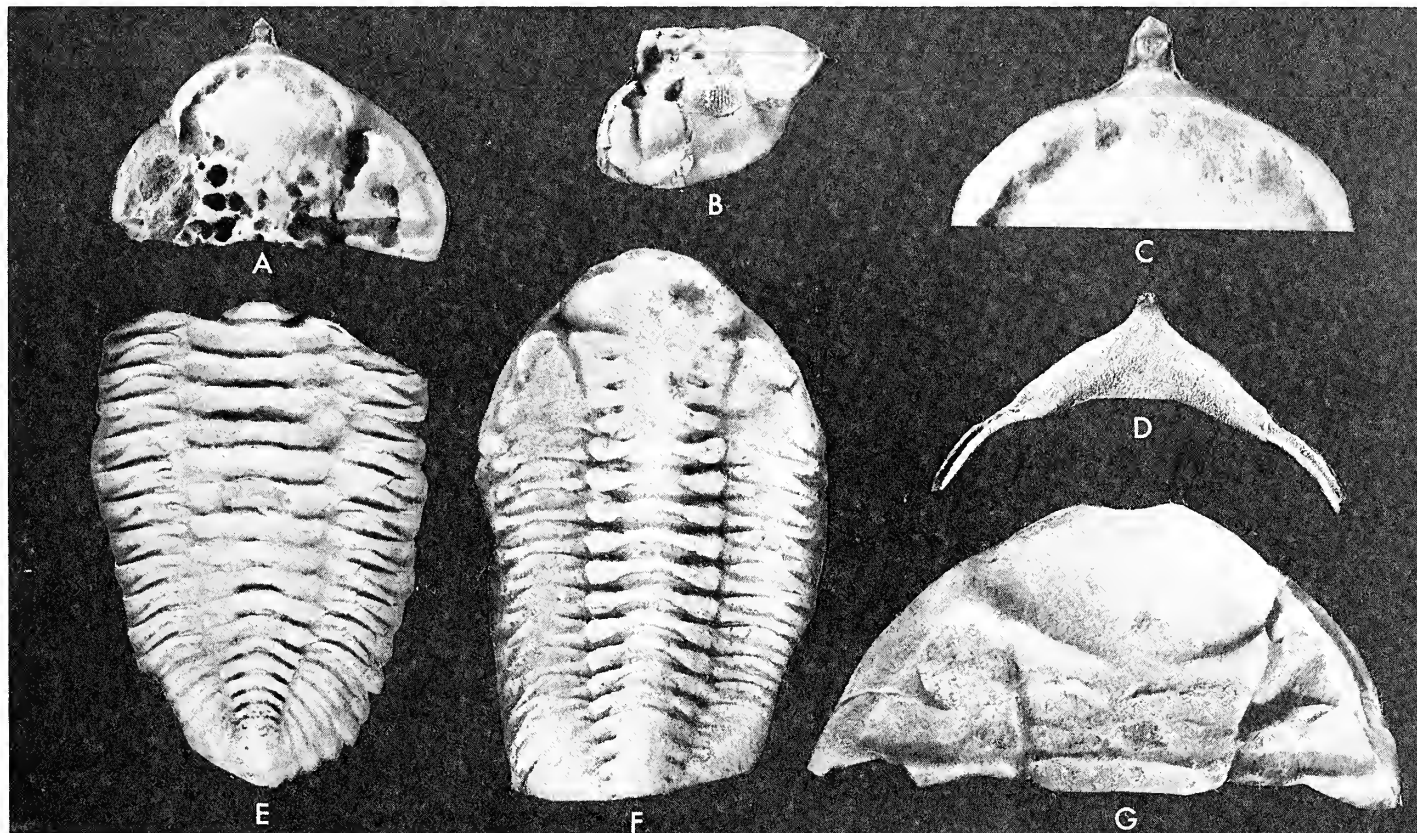


Plate 7. A-G, *Metacryphaeus allardyceae* (Clarke, 1913). Fox Bay Formation, West Falkland, A-C, E, Pebble Island; D, G, Fox Bay; F, Mount Robinson, Chartres River. A, B, dorsal and lateral views of cephalon, internal mold with traces of cuticle, syntype NYSM 9697, $\times 1.5$; C, detail of A, showing cephalic anterior border process, $\times 3.2$; D, ventral view of cephalic border, internal mold, NYSM 9720 (syntype of *Dalmanites falklandicus* Clarke, 1913), $\times 2$; E, dorsal view of outstretched thoracopygidium, latex cast from external mold, syntype NYSM 9698, $\times 1.5$; F, dorsal view of outstretched exoskeleton, internal mold, hypotype NYSM 9645, $\times 1.5$; G, dorsal view of cephalon, internal mold, NYSM 9719 (syntype of *Dalmanites falklandicus* Clarke, 1913), $\times 2$.

lectotype of *B. falklandicus* is at least partly fragmented; in this segment, the axial ring is shortened sagittally and raised as an angular crest. There is, however, no evidence for a sagittal spine on this segment, in contrast to the long, broad-based spine in this position (as well as on other rings) in *B. nilesi* n. sp. If thoracic axial spines are indeed completely lacking in *B. falklandicus*, this is a unique condition of this species of *Bainella*.

BAINELLA NILESI n. sp.

Plate 8

Dalmanites (*Mesembria*) *acacia* (Schwarz). CLARKE, 1913a, p. 116, Pl. 5, figs. 5-9.

Dalmanites acacia (Schwarz). CLARKE 1913b, Pl. 4, figs. 1-4.

Bainella sp. STRUVE, 1959, p. 485, Fig. 383, 2e.

Bainella (*Bainella*) "*acacia*" (Clarke) (*non* Schwarz). ELDREDGE AND BRANIŠA, 1980, fig. 4.

Diagnosis.—*Bainella* species with moderately deep impression of S2 and S3. Genal spine long, slender, nearly straight for most of length, weakly curved inward distally. Pygidial terminal spine long, slender, upturned.

Description.—Cephalon subtrigonal in outline, length (sag.) 55-60% of width across "advanced genal spine." Ventral margin with moderate anterior arch. Cephalic anterior border nearly flat, vertical, short medially, uniformly lengthens exsagittally, and projects at most slightly outside cranial anterolateral margin. Anterior furrow shallow to obscure. Preglabellar furrow shallow (sag., exsag.); cranial anterior border

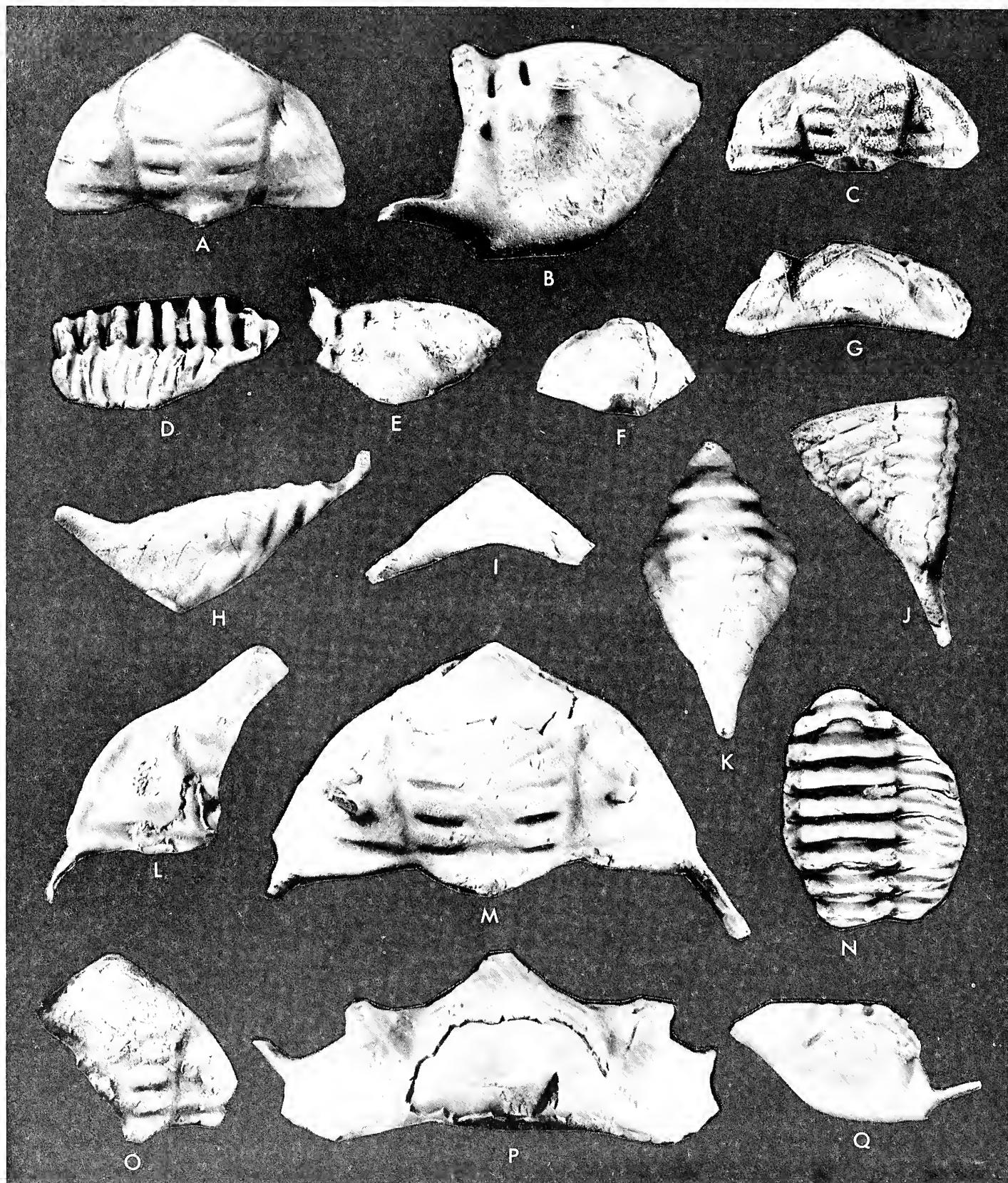


Plate 8. A-Q, *Bainella nilesi* n. sp. Fox Bay Formation, Pebble Island, West Falkland. A, dorsal view of cephalon, internal mold, paratype NYSM 16123, x1.5; B, M, P, lateral, dorsal, and anterior views of partly exfoliated cephalon, holotype NYSM 5628, x1.5; C, G, dorsal and anterior views of cephalon, internal mold, paratype NYSM 16124, x2; D, N, lateral and dorsal views of partial thorax, internal mold, paratype NYSM 16125, x1.5; E, O, lateral and dorsal views of partial cephalon, plastic cast from external mold, paratype NYSM 9715, x1.5; F, posterior view of pygidium, internal mold, paratype NYSM 16126, x1.5; H, K, lateral and dorsal views of partial pygidium, latex cast from external mold, paratype NYSM 16127, x2; J, ventral view of cephalic doublure, internal mold with some cuticle, paratype NYSM 16128, x1.5; J, dorsal view of pygidium, largely exfoliated, paratype NYSM 16129, x1.5; L, Q, dorsal and lateral views of partial cephalon, internal mold with some cuticle, paratype NYSM 16130, x2.

short (exsag.), extended sagittally as short triangular process. Anterior branch of facial suture runs ventrally from δ to just outside anterolateral corner of frontal lobe with nearly straight medially inflected course, then curves rather sharply inward; anterior margin of cranium gently arched (tr.) medially. Axial furrow shallow, narrow, straight, weakly divergent forward; distinct shallow depression opposite anterodistal edge of L3 (homologue of anterior pit).

Glabellar length 90-100% of width across frontal lobe; glabella gently and uniformly convex (sag.) or with posterior region (L1 to posterior third of frontal lobe) in nearly flat (sag.), gently inclined plane; glabella highest on posterior part of frontal lobe and raised above eye. Frontal lobe declined anteriorly with gentle to moderate uniform convexity (sag.); auxilliary impression system of paired rows of scars radiating from shallow, round posterior median impression. L2-L3 gently, evenly arched (tr.); L1 slightly more convex. S3 shallower than S2, faintly sinuous, proximal moiety nearly straight, distal moiety not confluent with axial furrow. S2 declined posteromedially and weakly sigmoidal, with proximal end flexed backward, moderately deep, non-apodemal, effaced distally. S1 straight, broad (tr.), with deep apodemal grooves; faintly declined posteromedially, nearly effaced sagittally and adjacent to axial furrow. L1 90-100% of length (exsag.) of L2. S0 shallow medially, deeply impressed distally as transverse apodemal grooves, shallows immediately adjacent to axial furrow; S0 longest sagittally, anterior margin curved forward, posterior margin poorly defined medially, evenly inclined to L0. L0 longest sagittally, about 25% of width, 75-80% of width of frontal lobe, strongly convex (tr.); occipital spine stout, transversely ovate, posteriorly deflected, raised well above posterior glabellar region.

Posterior branch of facial suture nearly straight, transverse between ϵ and lateral border furrow; sharply flexed back across lateral border, ω well behind ϵ . Anterior edge of eye opposite mid-distal part of L3, connected to axial furrow by short, thin ocular ridge; posterior edge of eye opposite posterodistal edge of L2. Large Eye Index about 0.30-0.35. Palpebral furrow shallow, of rounded V-shape; palpebral lobe reniform, moderately inflated above visual surface. Visual surface of twenty-three to twenty-four dorsoventral lens files, maximum of six to seven lenses per file; outer face of visual surface slightly concave, overhung by thin ridge along distal edge of palpebrum.

Interocular fixigena gently sloping up to palpebrum. Gena inclined nearly vertically, weakly dished beneath eye, steeply sloping to shallow lateral border furrow. Genal field with pervasive coarse dimpling. Lateral border evenly broadening toward midlength (exsag.) of gena, moderately convex. Blunt triangular spine ("advanced genal spine") at ω .

Cephalic posterior border furrow approximately straight, gently inclined abaxially, broad, moderately deep between axial furrow and behind outer edge of eye, shallowing distally, faintly continuous with lateral border furrow. Posterior border short (exsag.), moderately convex adjacent to axial furrow, rather strongly lengthening and flattened toward base of genal spine. Genal spine set inward of cephalic posterolateral margin, diverging posterolaterally (exsag.) at about 35° , gently flexed dorsally; spine evenly tapering, weakly curved inward distally.

Coarse granulation pervasive on cephalic cuticle except for glabellar furrows, axial furrow, and proximal part of posterior border furrow; granulation densest on doublure and borders.

Cephalic doublure longest sagittally, flattened, gently convex beneath distal part of axis; doublure narrow along most of gena, broadened beneath "advanced genal" and genal spine, sharply tapering inward of genal angle. Hypostomal suture gently convex forward.

Thorax gently tapering backward, composed of at least ten seg-

ments. Axial ring shortest sagittally, moderately convex (tr.); posterior margin of ring approximately transverse, anterior margin convex backward. Axial spine on each ring is long, broad-based, anteroposteriorly compressed, tapering to narrow, circular section. Ring furrow long (sag.) and shallow; transverse apodemes extend well inward of axial furrow. Articulating half-ring set well below crest of axial ring (even excluding axial spine). Inner part of pleurae weakly declined outward; outer part gently flexed backward, moderately turned down, with smooth curvature at break in slope (tr.); posterior ribs turned down proximal to axial furrow. Pleural furrow moderately deep and broad with approximately straight, oblique course across rib that runs proximally behind articulating facet. Articulating facet long (exsag.) on distal part of anterior thoracic segments. Pleural terminae incompletely known. Axial ring and pleural rib with pervasive coarse granulation.

Pygidium small, triangular, length (excluding terminal spine) about 70% of width; lateral margins approximately straight, flexed backward posteromedially as long, broad-based, tapering terminal spine. Axial furrow shallow, converges acutely backward, obscure posteriorly. Axis about 40% of pygidial width anteriorly, composed of eight or nine complete rings plus blunt, round-tipped terminal piece; anterior rings shorten gradually sagittally; axis weakly convex (sag.), moderately arched across anterior rings, gently convex (tr.) posteromedially. Rings densely covered with coarse granules; ring furrows smooth. Ring furrows transverse, shallow; anterior two ring furrows deepen adjacent to axial furrow, non-apodemal. Narrow, moderately deep pleural furrows impressed on cuticular surface in anterior four ribs; fifth and sixth (sometimes seventh) pleurae weakly defined. Inner part of pleurae moderately turned down and back; outer part more strongly turned down, with nearly flat (tr.) surface. Doublure flat beneath proximal part of terminal spine.

Discussion.—Clarke's (1913a, 1913b) identification of *Bainella* from the Fox Bay Formation as *Phacops acacia* Schwarz was regarded as dubious by Rennie (1930) and several subsequent workers (see Eldredge and Braniša, 1980, p. 202). Cooper (1982) synonymized *Bainella acacia* with *B. africana* (Salter, 1856), a conclusion that is supported herein on the basis of examination of a latex of the holotype of *B. acacia*. He also regarded Clarke's Falkland Island "*acacia*" material as questionably conspecific with *B. africana*. The assertion that differences in material from the Gydo Formation are "doubtfully of specific importance" (Cooper, 1982, p. 133) is not followed herein. Certain of the differences noted by Cooper (slightly deeper S2-S3, and longer genal spines in the Fox Bay specimens) exceed the range of variation in South African material. Furthermore, there is no evidence to support the suggestion that Eldredge and Braniša's (1980) reconstruction is erroneous with respect to the genal spines. Cooper (1982, p. 133) inferred that the long, nearly straight genal spines "were probably curved inward distally." However, their curvature is less than that shown by *B. africana*. Additional specimens (see Plate 8, figure L) have genal spines comparable with those illustrated by Eldredge and Braniša; the distal-most tip has a slightly greater curvature than the more proximal part of the lengthy spine. This faintly convex-outward form and posterolateral divergence contrasts with the hook-like, strongly back-curved genal spines of specimens from the Gydo Formation. Although some specimens of *B. africana* have fewer dorsoventral lens files in the visual field (twenty to twenty-one) than observed in *B. nilesi* (twenty-three to twenty-four), this is not a consistent difference; Reed (1925, p. 125) reported twenty-two to twenty-four files in *B. africana*.

The most obvious differentium between *Bainella nilesi* n. sp. and *B. africana* (Salter), however, is in the morphology of the pygidial termi-

nus. In *B. africana*, the tip of the axis is close to the pygidial posteromedian margin. As Cooper (1982, p. 131) noted, some specimens appear to have the axis extended beyond the margin, and no terminal spine is developed. *Bainella nilesi* n. sp. has an upturned mucro that extends far beyond the axial terminus (Plate 8, figures H, K), a condition shared with some other species of *Bainella* (e.g., *B. cristagalli* (Woodward)). The Falkland form is accordingly regarded as an allopatric species that is distinct from *B. africana*.

Etymology.—In honor of Niles Eldredge, for getting me into this mess.

Type material.—Holotype cephalon NYSM 5628 (Eldredge and Braniša, 1980, fig. 4), from the Fox Bay Formation, Pebble Island, West Falkland. Paratypes NYSM 9715 (Clarke, 1913a, Pl. 5, fig. 5), NYSM 9717 (Clarke, 1913a, Pl. 5, figs. 7, 8), NYSM 9718 (Clarke, 1913a, Pl. 5, fig. 9), NYSM 16123 (Clarke, 1913a, Pl. 5, fig. 6), figured specimens NYSM 16124-16130. All from the type locality.

Other material.—Unfigured topotypes NYSM 16148-16164, seventeen internal molds of cephalon (some partly cuticular); NYSM 16165-16167, three external molds of cephalon; NYSM 16168, internal mold of thoracopygidium; NYSM 16169-16170, two internal molds of pygidia; NYSM 16171, one counterpart mold of pygidium; BM IN 28174, internal mold of thoracopygidium; BM IN 28183, internal mold of partial cephalon, partly cuticular; all from Fox Bay Formation, Pebble Island. BM IN 46517, counterpart mold of partial cephalon, from Fox Bay Formation, Chartres Settlement, West Falkland.

Genus DELTACEPHALASPIS Eldredge and Braniša, 1980

Subgenus DELTACEPHALASPIS Eldredge and Braniša, 1980

Type species.—*Deltacephalaspis (Deltacephalaspis) comis* Eldredge and Braniša, 1980, by original designation.

DELTACEPHALASPIS (DELTACEPHALASPIS) MAGISTER

Eldredge and Braniša, 1980

Plate 5, figures A, B

Deltacephalaspis (Deltacephalaspis) magister ELDREDGE AND BRANIŠA, 1980, p. 221, fig. 13.

Material studied.—External mold of hypostome and cephalic double; internal mold of thoracopygidium AMNH 44158 from the

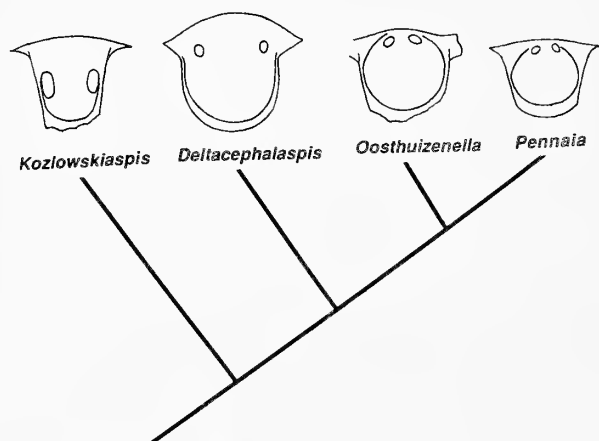


Figure 3. Transformation series for position of hypostomal maculae and relationships for genera of the "Calmonia group" of Eldredge and Braniša (1980). *Kozlowskiaspis subseiva* based on drawing of Clarke (1913a, Pl. 7a, fig. 3); other species based on specimens figured in this paper.

Scaphiocoelia Zone, Colchani, La Paz Department, Bolivia.

Description of hypostome.—Length (sag.) about 60% of width. Middle body ovate in outline, length 113% of maximum width (at midlength), with moderate, even convexity (tr.). Anterior margin moderately convex forward in front of middle body, faintly concave along margin of anterior wing. Wing broad, steeply inclined, with curved outer face lacking wing process. Anterior border furrow obscure, especially sagittally. Anterior lobe about 65% length of middle body, densely covered with coarse, low muscle impression scars. Middle furrow broad, shallow, separates weak convexity (sag.) of anterior and posterior lobes medially. Maculae large, ovate, distinctly displaced inward from lateral border furrow; front of macula just behind anterior wing, midlength at 33% of hypostomal length to posterior border furrow. Border furrow shallow laterally and posteromedially, moderately incised posterolaterally. Lateral and posterior borders narrow; pair of posterolateral marginal spines possibly present.

Discussion.—The hypostome of *Deltacephalaspis* was not known to Eldredge and Braniša (1980). That of *D. (D.) magister*, described above, is generally similar to the hypostome of *Bainella africana* in its moderate transverse arching of the middle body and narrow borders. Incision of the middle furrow is comparable to Cooper's (1982) *Bainella* hypostome. However, the maculae of *Deltacephalaspis* are displaced farther forward and adaxially than in *Bainella* or *Kozlowskiaspis* Braniša and Vaněk (see Eldredge and Braniša, 1980, fig. 27F, G); the latter genera were allied by Cooper (1982, p. 63) with *Deltacephalaspis*. This displacement appears to be a trend toward the apomorphic condition of *Pennaia* and *Oosthuizenella*, in which the maculae are close to the anteromedian margin of the middle body (Figure 3). This character supports the contention that *Deltacephalaspis* is closely related to *Pennaia* and *Oosthuizenella* (e.g., as parts of the "Calmonia group" of Eldredge and Braniša, 1980).

Genus METACRYPHAEUS Reed, 1907

Type species.—*Phacops caffer* Salter, 1856, by subsequent designation of Rennie, 1930.

METACRYPHAEUS ALLARDYCEAE (Clarke, 1913)

Plate 7

Cryphaeus? aliardyceae CLARKE, 1913a, p. 114, Pl. 4, figs. 7, 8; 1913b, Pl. 5, fig. 6.

?*Schizostylus (Curuyella) allardyceae* (Clarke). ELDREDGE AND BRANIŠA, 1980, p. 228.

Schizostylus? allardyceae (Clarke). COOPER, 1982, p. 167.

Dalmanites falklandicus CLARKE, 1913a, p. 105, Pl. 5, figs. 1, 2; CLARKE, 1913b, Pl. 4, fig. 5 (in part).

Calmonia ocellus (Lake). CLARKE, 1913a, Pl. 5, fig. 10; 1913b, Pl. 7, fig. 8 (in part).

Discussion.—*Metacryphaeus* specimens from the Fox Bay Formation are most similar to *M. caffer* (Salter) from the Bokkeveld Group and show little departure from the range of variation in that species as revised by Cooper (1982). Because *Metacryphaeus* is known from only a few specimens from several localities of the Fox Bay Formation on West Falkland Island, the taxonomic significance of the observed variation is difficult to assess. However, a rather broad range of intraspecific variation is observed in related species (see Lieberman et al., 1991). Taxonomic differentiation of the South African and Falkland samples appears, however, to be possible on the basis of the position of the eye. In cephalon from the Fox Bay Formation that have undergone minimal lateral distortion, the outer edge of the visual field

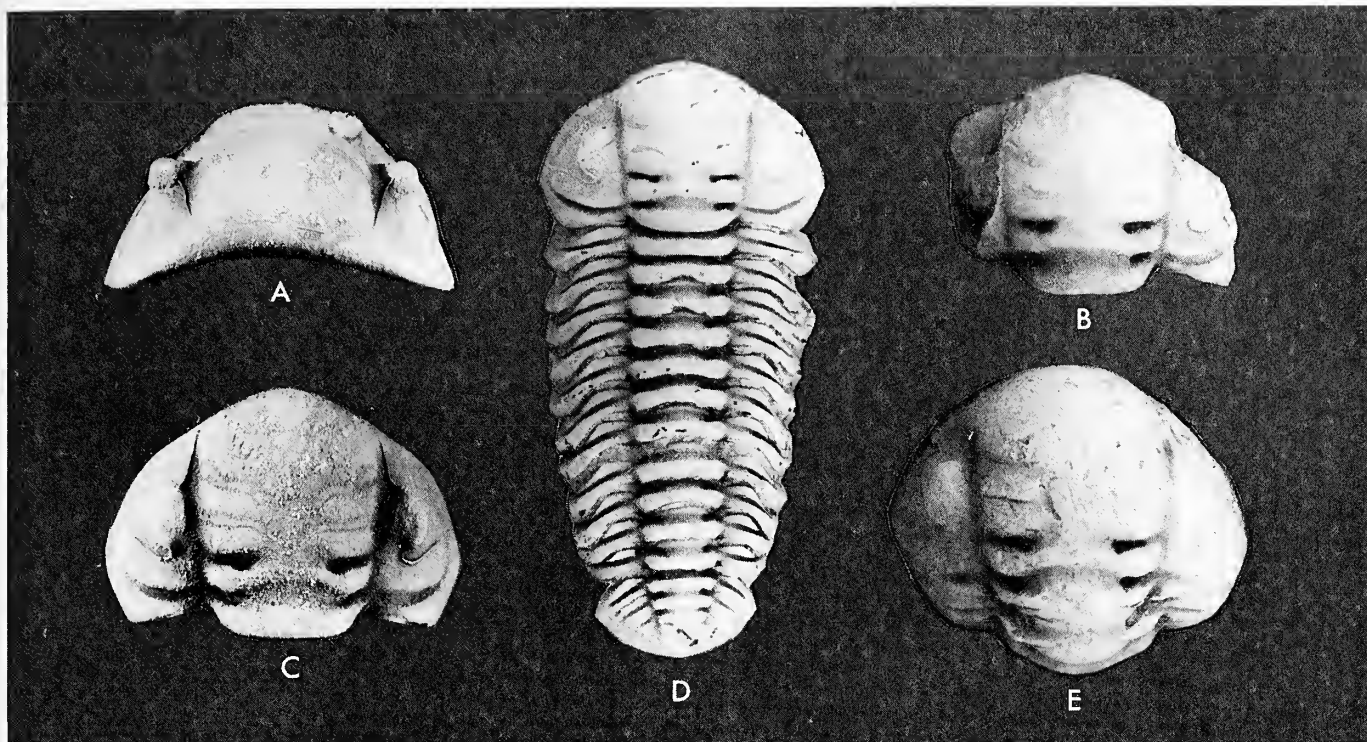


Plate 9. A-C, E, *Pennaia verneuili* (d'Orbigny, 1842). Icla Formation, Padilla, Chuquisaca Department, Bolivia, except possibly E, locality uncertain. A, C, anterior and dorsal views of cephalon, internal mold, hypotype AMNH 44171, x2; B, dorsal view of cephalon, internal mold, hypotype MNHN R50924, x2.1; E, dorsal cephalic view of enrolled exoskeleton, internal mold, lectotype MNHN R50921, x2; D, *Pennaia* sp. Icla Formation, Totorá, Cochabamba Department, Bolivia. Dorsal view of outstretched exoskeleton, internal mold, hypotype MNHN R50922 (figured Kozłowski, 1923, Pl. 4, figs. 1, 1a), x2. Photos for figures B, D, and E courtesy of J.-L. Henry (Rennes).

is located next to the lateral border furrow. South African specimens of *M. caffer*, by contrast, have the eye separated from the border furrow by a variably broad region of gena. In addition, the free lappets of the pygidial pleurae (Plate 7, figure E) are shorter and blunter in specimens from the Falklands than in Cooper's (1982) figured material. In this respect, pygidia from the Falklands resemble many South American specimens of *M. tuberculatus* (Kozłowski). These differences (and others noted below) are regarded as of specific value. *Metacryphaeus allardyceae* (Clarke, 1913) is an available name for the Fox Bay form, and indicates an earlier occurrence of the genus than that of *M. caffer* in the Voorstehoek Formation in South Africa.

Clarke (1913a) suggested that the complete thoracopygidium (Plate 7, figure E) and weathered cephalon (Plate 7, figures A-C), on which his *Cryphaeus?* *allardyceae* was based, were parts of the same individual. This view is followed herein, largely for Clarke's reasons (corresponding size and sole co-occurrence in a nodule). In addition, traces of the cephalic cuticle remain; the coarsely granulate prosopon (indistinct on the internal mold) corresponds in size and density with the thoracopygidial prosopon on the associated syntype (as well as that on the cephalon of NYSM 9719 from Fox Bay). Finally, the poorly preserved cephalon is typical of *Metacryphaeus* (in apparent form and spacing of the glabellar furrows, eye size and position, and genal morphology), to which the well preserved thoracopygidium is assigned without question (i.e., Eldredge and Ormiston, 1979, p. 159).

Earlier workers' referral of the "*Cryphaeus?*" *allardyceae* cephalon to *Schizostylus* Delo is based on Clarke's (1913a, Pl. 4, fig. 7; 1913b, Pl. 5, fig. 6) reconstruction of a long, slender anteromedian border spine. This reconstruction is, however, a gross exaggeration. The anteromedian process is indeed triangular and relatively narrow, but its elongation only moderately exceeds that observed in some individuals

of *Metacryphaeus tuberculatus* (Kozłowski, 1923) and *M. caffer*. This is a variable character within these species. However, an internal mold of the cephalic doublure (Plate 7, figure D) from Fox Bay also shows a triangular anteromedian process. Its consistent shape appears to be of utility in distinguishing *M. allardyceae* as a distinct species. A strong circular furrow developed along the narrow genal doublure is similar to that of *M. tuberculatus* (see Wolfart, 1968, Pl. 17, fig. 7b). In *M. allardyceae*, S3 is more weakly incised proximally than in *M. tuberculatus*. The thoracic axial rings of the "*allardyceae*" syntype are of more constant length (sag. versus exsag.) than those observed in the Mount Robinson specimen of *M. allardyceae* (Plate 7, figure F). In the latter specimen, the rings are markedly constricted sagittally. The variability of this feature in South African *M. caffer* suggests that this is also intraspecific variation.

Material.—NYSM 9645 (Clarke, 1913a, Pl. 5, fig. 10), Mount Robinson, Chartres River; NYSM 9719 (Clarke, 1913a, Pl. 5, fig. 1), NYSM 9720 (Clarke, 1913a, Pl. 5, fig. 2), Fox Bay; syntypes NYSM 9697, 9698 (Clarke, 1913a, Pl. 4, figs. 7, 8), Pebble Island. All specimens from the Fox Bay Formation.

Biogeography

The taxonomic cladogram for *Bainella* in Figure 2 can be examined from the perspective of the group's geographic differentiation. An area cladogram (Figure 4) was derived by substituting areas of geographic occurrence for the species. A few general statements on area relationships can be made on the basis of this branching diagram. On the one hand, South Africa and the Falklands are an area of endemism; on the other, South Africa shares its most recent history with the Andean shelf.

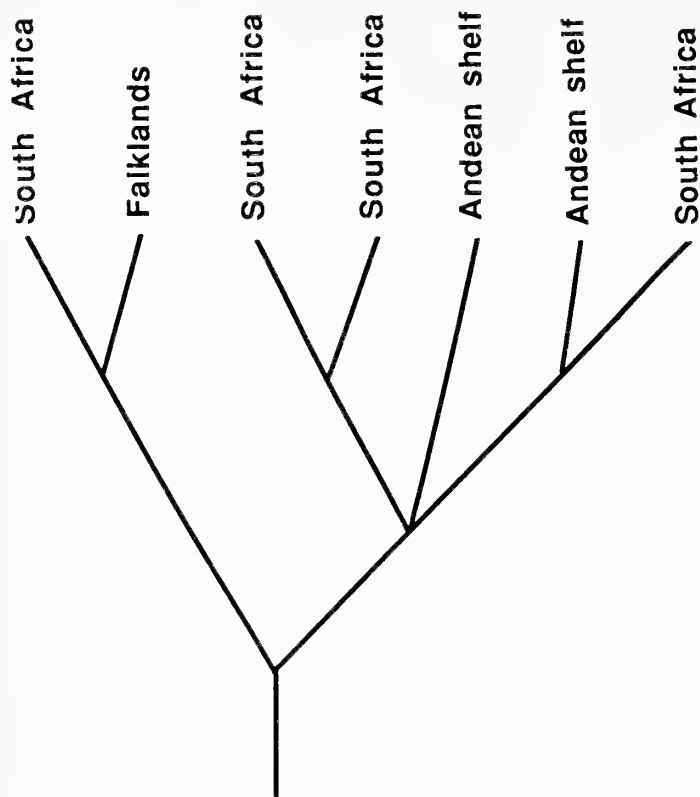


Figure 4. Area cladogram derived from *Bainella* species' relationships (see Figure 2).

Failure to detect a single pattern could be taken to imply that South Africa is an area with complex history (sensu Grande, 1985); its alternative relationships (with the Falklands and Andean shelf) might indicate patterns of different ages. It is plausible that, unlike the cladistic relationships of taxa (which are inferred to converge on a single pattern of historical relationships), geographic areas might have different cladistic relationships through time (Cracraft, 1988).

Area relationships predicted by *Bainella* can be compared with those retrieved from the spatial differentiation of other taxa that occur in these areas of the Malvinokaffric Realm. The proposal that *Oosthuizenella* and *Pennaia* form a more inclusive monophyletic group (Figure 3) offers this clade for comparison. Figure 5A depicts the cladistic relationships of these taxa, on which a few systematic comments are required. Cooper's (1982, p. 77) suggestion that "very similar" *Pennaia pauliana* Clarke, 1913 and *P. pupillus* (Lake, 1904) are closest relatives is accepted herein. Photographs of Clarke's types of *P. pauliana* show apomorphies that are shared with *P. pupillus*; these include a strongly bifurcate proximal end of S1, with a short posteriorly directed branch. Similarly, a sister group relationship is inferred for a species of *Pennaia* that occurs in the Icla-Padilla and Belén-La Paz-Sicasica regions of Bolivia (Icla and Belén-Sicasica Formations, respectively). The Belén-Sicasica species is distinguished by a number of characters: strongly shouldered genae, larger eyes (Large Eye Index 0.38-0.45, averaging 0.41), S2 convex forward, and lack of pygidial marginal denticles (see Kozłowski, 1923, Pl. 4, fig 3; Wolfart, 1968, Pl. 21, figs. 4-6, Pl. 22, figs. 1-7; Eldredge and Braniša, 1980, fig. 18B, C). This species also occurs at Totorá, Cochabamba Department (Plate 9, figure D) in beds assigned to the Icla Formation (Isaacson, 1977).

The lectotype of *Pennaia verneuili* (d'Orbigny, 1842) (Plate 9, figure E) is comparable to the Icla-Padilla species in its weak genal shouldering, small eyes (Large Eye Index 0.31-0.40, averaging 0.35), and

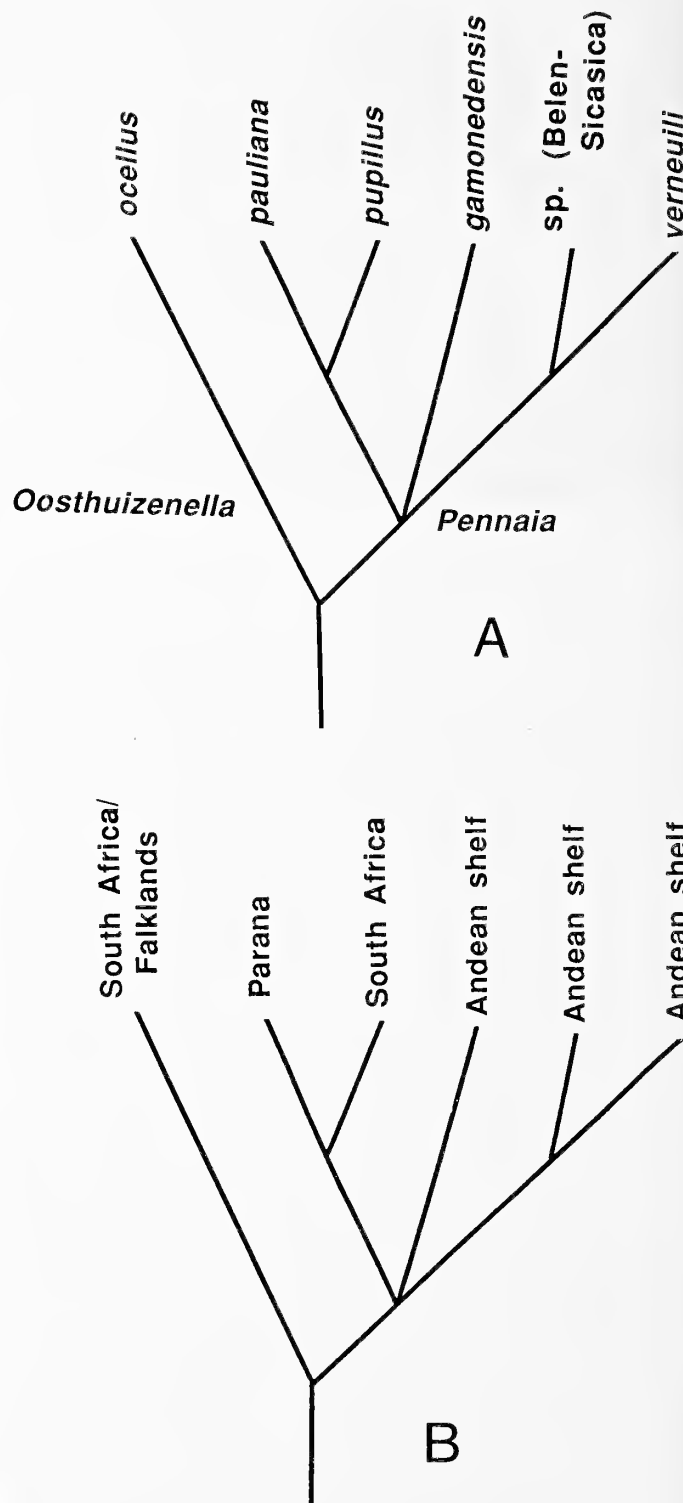


Figure 5. Taxonomic and area cladograms. A, Taxonomic cladogram for the sister taxa *Oosthuizenella* + *Pennaia*. B, Area cladogram derived from Figure A.

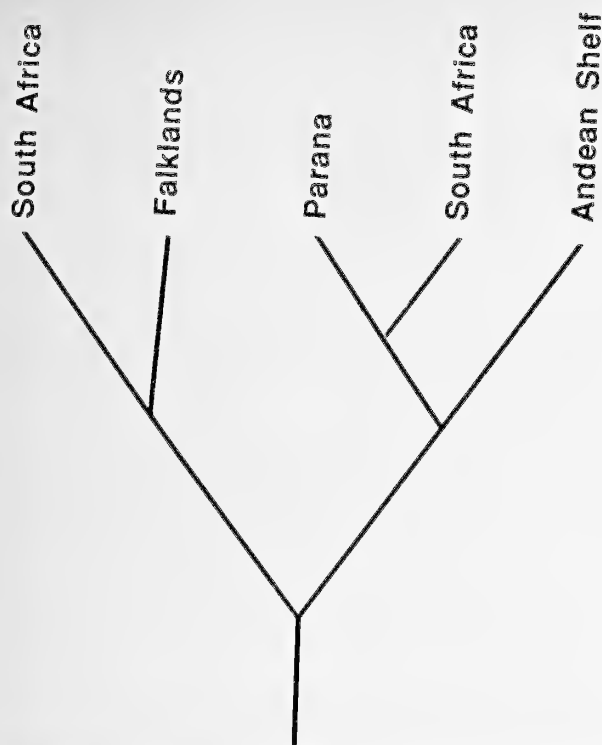


Figure 6. General area cladogram. Consensus of informative components in Figure 4 (area cladogram from *Bainella*) and Figure 5B (area cladogram from *Oosthuizenella* + *Pennaia*).

straight S2 (e.g., Kozłowski, 1923, Pl. 4, figs. 4-6; Wolfart, 1968, Pl. 22, figs. 8-9, Pl. 23, figs. 1-3; Eldredge and Braniša, 1980, fig. 18D, 29C; Plate 9, figure A-C). Because the provenance of d'Orbigny's type is unknown, Wolfart's (1968, p. 116) proposal of a type locality for *P. verneuili* in the Belén Formation is doubtful. It appears that *Pennaia acutiloba* (Knod, 1908), from the Icla Formation is a junior subjective synonym of *P. verneuili*, and the Belén-Sicasica species typically assigned to *P. verneuili* is an undescribed form ("sp. Belén-Sicasica" in Figure 5A). Another species, *Pennaia gamonedensis* (Eldredge and Braniša, 1980), has ambiguous relationships within the genus.

This taxonomic cladogram leads to the area cladogram in Figure 5B. *Oosthuizenella ocellus* is undifferentiated in South Africa and the Falklands; its sister group includes a Paraná-South African component that has an Andean sister group.

Comparison of Figures 4 and 5B indicates a congruence between the historical patterns predicted by the two groups. This geographic congruence (Nelson and Platnick, 1984) is taken to imply a common history. Components that are consistent between both cladograms are shown in the general area cladogram of Figure 6. The South Africa-Falkland component is determined by *Bainella*, whereas *Oosthuizenella* is widespread (uninformative) in these areas. Historically, it is inferred that *Bainella* responded (i.e., differentiated/speciated) to a vicariant event that left *Oosthuizenella* unmodified. However, the widespread species is consistent with the sister area relationship indicated by the differentiated species. The more informative resolution provided by *Bainella* is entered into the consensus (cf. Nelson and Platnick, 1981). As noted above, *Metacryphaeus* replicates this information; the Falkland form (*M. allardyceae*) is most closely related to South African *M. caffer*.

An alternate pattern of relations for the South African fauna is consistently indicated by species of each group. The area cladogram based on *Bainella* predicts closest relations of some South African species with those of the Andean shelf (Figure 4). Similarly, *Pennaia* has an Andean-South African occurrence and provides additional information that the latter area is more closely related to the Paraná Basin (Figure

5B) than to the Andean shelf. The general cladogram (Figure 6) includes this more informative resolution of the Andean-South African-Paraná region.

These alternate relations for the Devonian of South Africa have been identified previously. Popp and Baldis (1989) restricted the Malvinokaffric Province to a South African-Falkland area of endemism, whereas Cooper (1982, p. 1) summarized the affinities of the South African fauna as "clearly with Bolivia." That both components are consistently replicated by different calmonioid taxa suggests that each reflects the historical affinities of the area. This is most plausibly inferred to reflect patterns of different ages. A minimum age for differentiation of the Andes-South Africa-Paraná area of endemism is provided by known occurrence of species of both clades (*Bainella insolita* and *Pennaia gamonedensis*) in the *Scaphiocoelia* Zone (late Siegenian?-Emsian; see Isaacson and Sablock, 1988) in Bolivia. The South African-Falkland component might be a younger (Emsian) overprinting of this. A minimum age for this component is given by the late Emsian date of the Gydo Formation (Cooper, 1986).

Acknowledgments

E. Landing kindly arranged loans of specimens in the New York State Museum collections. I thank N. Eldredge, J.-L. Henry, B. Lieberman, and R. Ludvigsen for comments on the manuscript. M. da G.P. de Carvalho and J.-L. Henry provided negatives of J.M. Clarke's and A. d'Orbigny's types, respectively. Assistance with specimen preparation and photography was provided by S. Klokak and A. Modell (Department of Invertebrates, American Museum of Natural History).

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Middle Cambrian mollusks from Idaho and early conchiferan evolution

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Abstract

Reconsideration of the morphologic relations among Cambrian and Ordovician conchiferan mollusks has led to a revision of phylogenetic relationships and systematics of the Conchifera in the Cambrian. This analysis supports the assumption that the presumed primary metameric segmentation of the hypothetical ancestor of the Conchifera has not persisted into Recent monoplacophorans. Pedal musculature was presumably fused in the earliest Cambrian limpet-shaped to high conical or gyroconic Conchifera, and a secondary serial arrangement of pedal muscles may have given rise to representative tryblidiacean taxa. Organisms with low, cap-shaped, patelliform shells with ring-shaped muscle scars may be identified as the ancestors of tryblidiaceans with multiple muscle scars. One example of such an organism is *Protoconchioides* emend., exemplified by *P. douli* n. sp. from the Middle Cambrian of Idaho. An advanced arrangement of the pedal musculature into discrete bundles is represented by *Protoconchioides? rasettii* n. sp. from the Middle Cambrian of British Columbia.

The revised phylogeny for helcionellid genera requires a class-level taxonomic category for which the term "Helcionelloida" was introduced recently (Peel, 1991). The term "Monoplacophora" is shown to be a junior synonym of Tryblidiacea, and the latter designation should not be used any longer. The resulting class-level grouping, which includes Tryblidiida and Bellerophonitida, is termed "Amphigastropoda."

The helcionellid genus *Latouchella* is discussed in detail. Additional descriptions deal with *Latouchella pocatelloensis* n. sp. and *L. arguta* (Resser, 1939) from Idaho. The following higher-level taxa are proposed: Helcionellida n. order, Hypseloconina n. suborder, Protoconchioididae n. family.

Introduction

A number of recent publications have dealt with the early history of the mollusks (e.g., Salvini-Plawen, 1972, 1980, 1981, 1985; Runnegar and Pojeta, 1974, 1985; Runnegar and Jell, 1976; Yochelson, 1978, 1979, 1988; Runnegar, 1981, 1983, 1985). They represent a modern approach to the early phylogeny of a group with one of the best fossil records. The mollusks may be the only large fossil group for which the divergence of major phylogenetic lineages can be clearly documented in the rock record. However, as the anatomy of soft parts is not readily

determinable from only the shell, we are far from a precise reconstruction of phylogenetic pathways and systematic relationships. In an earlier report, Geyer (1986) evaluated the systematic position of various groups that were formerly believed to belong to the Class Monoplacophora. A few Middle Cambrian mollusks from Idaho, which are described below, provide an opportunity to illustrate and update some of these ideas and, in particular, to re-evaluate the systematic relationships of helcionellaceans and tryblidiaceans.

During review of this manuscript, an article by Peel (1991) that dealt with the same subject was published. This article comes to similar conclusions from a slightly different viewpoint. A few aspects of this report may seem to be superseded for the readers of Peel's article, but are retained herein.

What is a monoplacophoran?

A major task in the tracing of molluscan evolution is the reconstruction of soft-part anatomy. Unfortunately, no obvious relationship exists between soft-parts and shell morphology among univalved mollusks. Over the years, the earliest univalved mollusks have been regarded as gastropods, monoplacophorans, or something unique. It is now possible to recognize perhaps a dozen different higher-ranked taxa (some of which may not be mollusks) among these superficially similar shells (e.g., Qian and Bengtson, 1989). However, the majority of univalved molluscan shells are presently grouped within the poorly defined Class Monoplacophora.

Modern Monoplacophora are characterized by a set of multiple, paired muscle scars that indicate the arrangement of the pedal musculature. In addition to multiple muscle cords, other soft parts (e.g., gills, auricles, and nephridia) in modern monoplacophorans share the multiple arrangement of the pedal musculature. The discovery of living *Neopilina* a few decades ago (Lemche, 1957) reinforced the concept of a Class Monoplacophora for a small group of Paleozoic cap-shaped shells characterized by multiple muscle scars.

Subsequently, the number of mollusks known from the Early Paleozoic, especially in the Early and Middle Cambrian, that obviously were not gastropods, grew rapidly. Most of these were assigned to the Class Monoplacophora, a large group of taxa with heterogeneous morphology that share only a univalved shell and a probable lack of torsion in the soft tissue. The lack of torsion is a shared primitive feature, and a univalved shell is the normal condition of organization among

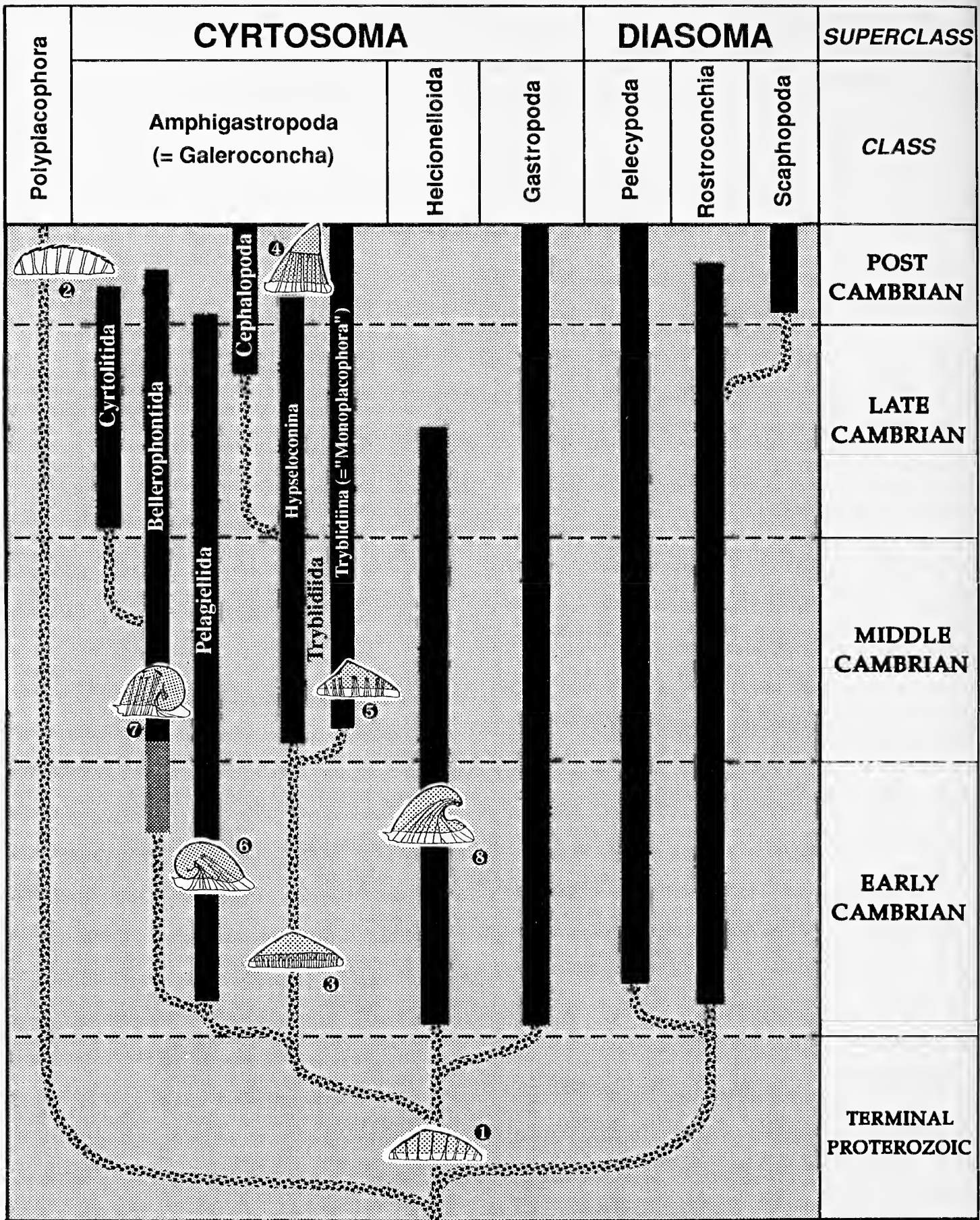


Table 1. Classification of the Conchifera proposed herein.

Infraphylum Conchifera Gegenbaur, 1878 (not Conchifera Lamarck, 1818)
Superclass Cyrtosoma Runnegar and Pojeta, 1974, emend. herein
Class Amphigastropoda Simroth <i>in</i> Wenz, 1940 (=Galeoconcha Salvini-Plawen, 1980, Tergomya Peel, 1991)
Order Pelagiellida MacKinnon, 1985 (=Pelagiellida Runnegar and Pojeta, 1985)
Order Bellerophontida Ulrich and Scofield, 1897 (=Belleromorpha Naef, 1911)
Order Cyrtolitida n. order (nom. transl. ex Cyrtolitidae Miller, 1889)
Order Tryblidiida Lemche, 1957
Suborder Hypseloconina n. suborder (nom transl. ex Hypseloconidae Knight, 1956; =Order Kirengellida Rozov, 1975 <i>pro parte</i>)
Suborder Tryblidiina Wenz, 1938 (=Monoplacophora Odhner <i>in</i> Wenz 1940, Subclass Tergomya Horny, 1965)
Class Cephalopoda Schneider, 1784 (=Siphonopoda Lankester, 1877)
Class Helcionelloida Peel, 1991
Class Gastropoda Cuvier, 1797
Superclass Diasoma Runnegar and Pojeta, 1974
Class Rostroconchia Pojeta, Runnegar, Morris, and Newell, 1972 (=Rostroconchida Cox, 1960 <i>pro parte</i> , Bivalvia Linné, 1758 <i>pro parte</i> .)
Class Pelecypoda Goldfuss, 1820 (=Bivalvia Linné, 1758 <i>pro parte</i> , Lamellibranchiata de Blainville, 1824)
Class Scaphopoda Bronn, 1862

Figure 1. Diagram of tentative phylogenetic radiation of the Conchifera. Black bars and hatched bars indicate proven and probable fossil records, respectively. Schematic organization shows attachment of pedal musculature for key groups: (1) Hypothetical ancestor of the Conchifera with primary metameric segmentation and concentrated dorsoventral musculature. (2) Loricatan polyplacophoran with serial arrangement of the dorsoventral musculature. (3) Primitive hypseloconinan, a *Protoconchioides*-like amphigastropod, with ring-shaped arrangement of the pedal musculature. (4) Hypseloconid amphigastropod with ring-shaped arrangement of the pedal musculature. (5) Tryblidiinan amphigastropod with secondarily derived concentrated pedal muscle cords. (6) Pelagiellid with two pedal muscle insertions (muscle scar on opposite side indicated by hollow signature). Note the exogastric coiling. (7) Bellerophontid with scattered pedal muscle insertions. (8) Helcionelloid with pedal musculature inserted at the apical area.

conchiferan mollusks. In addition, multiple muscle scars are absent in the interior of the conchs of most early mollusks.

The only character in Cambrian molluscan shells that provides information about the organization of the soft body is the presence and distribution of muscle scars. Geyer (1986) argued that cyrto- or gyroconic Conchifera whose soft parts had not undergone torsion should have more prominent muscle scars than do typical helcionellids. However, the earliest shells with conspicuous muscle scars are known from Middle Cambrian strata. These specimens were earlier assigned to *Scenella* (Rasetti, 1954) and are tentatively assigned to *Protoconchioides* herein (see below). Cap- or limpet-shaped shells are present in earliest Cambrian strata, but even well-preserved specimens do not have the very distinct muscle imprints that are known in tryblidiaceans. Reports of muscle scars in earliest Cambrian limpet-shaped shells deserve careful examination; perhaps some of those taxa should be excluded from the Mollusca (e.g., *Trucatoconus yichangensis* Yu, 1979; compare Yu, 1987, Pl. 28). Apart from these, a few limpet-shaped shells show a weak circular muscle imprint similar to that found in *Protoconchioides douli* n. sp. (described below). These taxa (e.g., "*Scenella radiata*" in Yu, 1979, Pl. 2) probably had a similar organization.

Runnegar (1981) presented a developmental scheme for shells and muscle scars within Ordovician monoplacophorans, and provided a comprehensive interpretation. However, if all the Early and Middle Cambrian helcionellaceans are assumed to belong to the Class Monoplacophora, the following three interpretations should be considered:

1. The earliest monoplacophorans had a soft-tissue organization that was not homologous to that of Ordovician through Devonian forms. Thus, two possibilities result: (1a) The pedal musculature indicated by multiple muscle scars had evolved secondarily and is not homologous to the primarily metameric pedal musculature of the "archetypal mollusk" ("Ur-Mollusk"). Thus the nature of the pedal muscles in the living monoplacophoran *Neopilina* Lemche, 1957 (a *musculus longitudinalis circularis*) need not be homologous to that of primitive gastropods. (1b) The multiple muscle scars of the Paleozoic monoplacophorans arose secondarily from a single pair of pedal muscles.
2. The limpet-shaped shells of the (early?) monoplacophorans with multiple muscle scars do not reflect a primitive organization. Thus an Early or Middle Cambrian limpet-shaped shell does not necessarily prove a non-torted *recte* "monoplacophoran" organization. The limpet shape of Cambrian univalved shells seems to suggest a morphological adaptation rather than a primitive organization of the soft parts. Evidence for this point of view is provided by the unusually great variability of shell size and shape (compare Branch and Marsh, 1978; Hartwick, 1981; Denny et al., 1985). A concise synopsis of limpet organization in gastropods with regard to adaptation and ecology was given by Branch (1985).
3. It would be expected that the highly convex shells of organisms with primarily metameric organization (as is assumed for the helcionellaceans) should have developed from very low conchs. If such flat-shelled mollusks with a morphology and organization similar to *Neopilina* (and providing a link between "Aplacophora" and Conchifera) ever existed, they were very short-lived and are currently not known as fossils. The earliest known shells are nearly identical in shape to the later helcionellaceans. The connecting link with the plan of a Recent monoplacophoran, as inferred by Salvini-Plawen (1980, 1985), would thus form a very early transition to a

plan with a bundled dorsoventral musculature and a single pair of gills.

The three interpretations outlined above remain highly debatable and cannot (yet?) help to identify the evolutionary pathways. However, "Occam's razor" would lead to the following conclusions based upon *Protoconchioides* Shaw, 1962:

Protoconchioides, as emended herein, comprises Early to Middle Cambrian limpet-shaped, nearly smooth shells that have a faint, ring-shaped muscle scar. The origin of this muscle scar is difficult to evaluate. Because of the relatively great age and presumed phylogenetic relationships of *Protoconchioides*, it may be assumed that the muscle ring reflects a primary, primitive arrangement of pedal muscles. Therefore, this animal was probably untorted. If such is the case, the multiple muscle scars of younger Middle Cambrian and later monoplacophoran-like mollusks could have been derived from the divided pedal musculature of a *Protoconchioides*-like stock. *Protoconchioides? rasettii* n. sp. has a set of distinct muscle imprints that seems to reflect an advanced state of organization of the pedal musculature. This would indicate that the multiple muscle scars of Early Paleozoic monoplacophorans developed from a single pair of pedal muscles and not from a set of serial muscles as in modern monoplacophorans. If the serial organization of the soft parts has the systematic significance that is generally assumed, it may even be doubtful that Paleozoic and Cenozoic monoplacophorans belong to the same order.

The term "Monoplacophora"

The Class Monoplacophora is nomenclatorically invalid even apart from the systematic heterogeneity of the group. However, only a few authors have recommended that the term "Monoplacophora" be abandoned (e.g., Salvini-Plawen, 1980; Wingstrand, 1985; Geyer, 1986; Peel, 1991). As argued by Salvini-Plawen (1980) and Geyer (1986), "Monoplacophora" was introduced as an informal term by Wenz (1940). Wenz (1940, p. 5) cited an oral communication by N.H. Odhner in which the name "Monoplacophora" was clearly understood to be an informal designation. Both Wenz and Odhner used the term to distinguish the shells of the tryblidiaceans from those of the polyplacophorans. Thus, "Monoplacophora" is an informal name for the Superfamily Tryblidiacea. In that same publication, Wenz (1940) clearly excluded the Bellerophontacea from this group. Consequently, the name "Monoplacophora" should not be applied to a class that unites the Tryblidiacea and Bellerophontacea and is inappropriate for systematic nomenclature. However, "Monoplacophora," as a grouping for the tryblidiaceans and bellerophontaceans, is the basis for the Class Monoplacophora Wenz in Knight, 1952.

Salvini-Plawen (1980, p. 254, 255) proposed the name "Galeoconcha" for a class that includes the orders Tryblidiida and Bellerophontida. However, the term "Galeoconcha" is a junior synonym of the Amphigastropoda. Simroth (1904) informally proposed the Class Amphigastropoda for bellerophontids as a way to separate them from the Gastropoda, but did not mention the tryblidiaceans. Wenz (1940, p. 9) revived the term and included the superfamilies Tryblidiacea and Bellerophontacea in the Subclass Amphigastropoda Simroth in Wenz (1940) and regarded both taxa as non-torted gastropods. The term "Amphigastropoda" is therefore available for the class, and it is proposed herein that the name be applied to the class that comprises the orders Tryblidiida, Bellerophontida, Pelagiellida, and Cyrtolitida (Figure 1). The Cephalopoda probably arose from the same stock.

Peel (1991) introduced the name "Tergomya" for a class with the same concept. The name was derived from the Subclass Tergomya Horný, 1965, which is more or less a synonym of the Suborder Tryblidiina Wenz, 1940. The class-level taxon Tergomya Peel, 1991, is thus a junior synonym of Amphigastrophoda Simroth in Wenz (1940).

Taxonomic groups

Tryblidiida

Only those species with conchs that possess serial muscle scars and an apex in an anterior position are morphologically comparable with modern monoplacophorans. Exceptions to this grouping can be found among Recent patellacean gastropods, in which the position of the apex is irrelevant for classification because it may change during ontogeny. Endogastric and exogastric coiling are represented in tryblidiaceans. Genera that meet the conditions listed above are the typical Tryblidiacea, such as the Late Cambrian to Early Ordovician *Proplina* Kobayashi, 1933; the Late Ordovician to Silurian *Pilina* Koken, 1925; and the Silurian *Drahomira* Perner, 1903. Such genera are included within the helcionellaceans as understood by Runnegar and Jell (1976), but their systematic position is doubtful, and they do not appear in the same stratigraphical interval with the other helcionellacean genera (which are almost exclusively Early and Middle Cambrian in age). Examples of such Cambrian helcionellaceans include *Archaeophiala* Perner, 1903; *Lenaella* Byalyj, 1973; and *Moyerokania* Rozov, 1970. In addition to the Cyrtolitiidae, the remaining "monoplacophorans" comprise only those taxa for which no muscle scars are known, apart from imprints in the apical part, and the shells of which are highly convex and mostly cyrto- or gyroconic.

Serial muscle scars are known from "*Scenella* sp. undet." of Rasetti (1954) from the Burgess Shale (Runnegar and Pojeta, 1985, fig. 11; for reconstruction see Runnegar and Pojeta, 1974, fig. 2). However, Rasetti (1957) and Yochelson (1978, 1979) have shown that these specimens do not represent a species of *Scenella*. The Burgess Shale specimens are closely related to known species of *Protoconchioides* and are tentatively assigned to that genus as *Protoconchioides? rasettii* n. sp. Yochelson (1979) pointed out that an erroneous concept of *Scenella* has developed over recent decades, and the concept of the genus has changed even further within recent years. A recent description of the genotype species *Scenella reticulata* Billings, 1872, was given by Landing (1988, p. 687-698, Fig. 12.1, 12.2). His figures seem to prove that *Scenella* is indeed a helcionellid mollusk (see Landing and Narbonne, 1992), and therefore that almost all other species assigned to *Scenella* must be removed from the genus, as well as the majority of them from the class. Some named species of "*Scenella*" probably represent opercula of unknown taxa; these include *Scenella undulata* Yu, 1981. Qian and Bengtson (1989) have tentatively placed *Scenella undulata* in synonymy with *Mobergella? bella* (He and Yang, 1982), which, in turn, is based in *Palaeacmaea bella*.

Bellerophontida

Uncertainty about the systematic position of bellerophontid mollusks arose from the debate over whether these animals were untorted or torted, and thus whether or not they were gastropods, as traditionally assumed (compare Harper and Rollins, 1982). However, a sinus, as well as symmetrically arranged muscle scars in a number of bellerophontid shells, indicates a symmetrical organization of pedal musculature and pallial organs. Thus these taxa must be regarded as untorted, as suggest-

ed in earlier reports (Salvini-Plawen, 1972, 1980; Runnegar, 1981). Moreover, Salvini-Plawen (1980, p. 254) considered planispiral coiling generally as "proof of an untorted condition." Nevertheless, the mantle cavity is in an anterior position, which in an advanced state requires a slit for maintaining a sufficient water current.

According to Runnegar (1981), the bellerophontid lineage arose from animals with a tryblidiid organization of serial muscles. However, the patterns of muscle scars in early bellerophontid shells may also have been derived from the circular pedal musculature of cap-shaped shells such as those of *Protoconchioides*.

Pelagiellida

If Runnegar's (1981) comprehensive and elegant interpretation of the musculature of *Pelagiella atlantoides* is accepted, the Order Pelagiellida must have been derived from the same stock as the Bellerophontida and Tryblidiida. The Bellerophontida have a clearly different arrangement of the pedal musculature. Although the Bellerophontida appear later in the fossil record, they cannot be derived directly from pelagiellids.

Several details of the shell morphology of *Archaeospira* Yu, 1979, and related asymmetrical shells that have been regarded as relatives of *Latouchella* seem to indicate a pelagiellid organization. These, then, should be grouped tentatively with the Pelagiellida. A pelagiellid organization for the *Archaeospira* group is indicated by the shell geometry. According to Linsley's (1977) laws, the shells had to be carried with the apical portion in an anterior position in order to balance the center of gravity over the midline of the cephalopodal mass.

Cyrtolitiids

Some of the cyrtolitiids have several paired muscle scars on the outer side of the spire. These scars are serially arranged in dorsal view. By analogy with the muscle scars of the tryblidiaceans, a concentric arrangement of the muscle insertions is expected. However, such a suspension of the soft body is probably unsuitable for functional reasons. An interpretation of the evolution of the muscle arrangement has been given by Runnegar (1981).

As shown by Bandel (1982), the development of the retractor muscles is a function of the shape of the shell, and thus of mode of life. Species that have flat, limpet-shaped shells preferred to live on a hard substratum. These species had to be able to attach tightly to the substrate, and multiple muscles would have been most effective and would have permitted a balanced transfer of muscle power. Creeping-vagile species with an elongate dorsoventral axis and, usually, a coiled shell would have retreated into the shell for protection. For these species, relatively few muscles would have been sufficient to retract the foot.

The configuration of the muscle scars in the Cyrtolitiidae therefore arose from a modified "monoplacophoran" body plan. This modification was used by Salvini-Plawen (1980) as the phylogenetic basis for considering the group as a suborder of his Order Tryblidiida.

Hypseloconiids

Hypseloconiids comprise a family-level grouping of genera with a ring-shaped constriction on the interior molds that corresponds to a U-shaped arrangement or paired discrete impressions of the retractor musculature (see Stinchcomb, 1980). Unfortunately, the shells of all of these genera are unknown. The pedal musculature was inserted relatively close to the apex. The orientation of the apex is somewhat inconstant, but the apex curves backward in more strongly conical specimens of *Hypseloconus* Berkeley, 1898. The genus *Knightoconus* Yochelson,

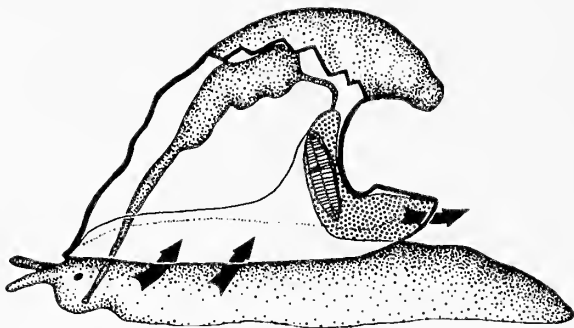


Figure 2. Schematic reconstruction of *Latouchella* Cobbold, 1921. Arrows indicate the direction of the water current. Mantle cavity partly extended laterally, dotted posteriorly, with a single pair of gills. Intestine simplified. Redrawn from Geyer (1986, Fig. 3).

Flower, and Webers, 1973, demonstrates that the Hypseloconidae preferably coiled in an endogastric manner. Thus the larger gap between the muscle scars in *Hypseloconus* is situated anteriorly as interpreted by Stinchcomb (1980). The widest insertion area was close to the posterior end. This may correspond to the attachment of the body in the tryblidiacean genus *Proplina* Kobayashi, 1933, which also has a U-shaped muscle scar. The apex is coiled endogastrically but is located anterior to the center of the shell.

For a long time, hypseloconids have been almost neglected. In recent years, Stinchcomb (1986) described six new genera, and Peel (1988) expanded the traditional concept of the hypseloconids when he assigned *Kirengella* Rozov, 1968, to the group. *Kirengella* was previously interpreted as a typical "monoplacophoran" with six pairs of muscle scars arranged in a U-shape and the apex directed toward the anterior margin of the shell (Rozov, 1968). Yochelson et al. (1973) presented a contrasting interpretation in which the apex was considered to be directed toward the posterior. Peel (1988) further discussed this problem of conch orientation. He concluded that the anomalous orientation of the apex (in comparison to the helcionellaceans) can be explained by an allometric growth similar to that in *Yochelcionella ostetata*. Therefore, the orientation of the muscle scars in *Hypseloconus* (and *Kirengella*) is comparable with those in such "true" tryblidiaceans as *Pilina*.

These characters do not provide a broad spectrum of morphological information. However, they indicate that the Hypseloconidae might have been derived either from a group that includes *Protoconchioides* or from the same stem group. Thus, the hypseloconids are raised to the Suborder Hypseloconina (new). In its external morphology, *Kirengella* is transitional between *Protoconchioides* and *Hypseloconus*.

Rozov (1975) proposed the Order Kirengellida that included the Family Romaniellidae, based on *Romaniella* Doguzhaeva, 1972. *Romaniella* was assumed to be a synonym of *Hypseloconus*, an interpretation that was not accepted by Peel (1988) and is not accepted herein. As Rozov's order naturally includes *Kirengella*, one might assume that the name "Kirengellida" could be applied for the systematic group proposed herein. However, the concept and the genera referred to Rozov's "Kirengellida" do not correspond to those of the new suborder. The name "Kirengellida" is thus inappropriate, and the Suborder Hypseloconina (new) is proposed herein.

Archinacellina

Earlier reports suggested that the Hypseloconidae were referable to

the Suborder Archinacellina rather than to the helcionellaceans. However, the systematic position of the Archinacellina is not yet clear. Although this suborder has been traditionally referred to the monoplacophorans, either to the Tryblidiacea (Runnegar and Jell, 1976) or as an Order Archinacelloidea (Knight and Yochelson, 1958), subsequent reports favored an assignment to the Gastropoda (e.g., Harper and Rollins, 1982). Yochelson (1988) recently considered a patellacean organization for the Family Archinacellidae, as indicated by a general similarity to the patellacean genus *Floripatella* Yochelson, 1988, from the Middle Ordovician of Utah. In addition to Yochelson's comments, it should be mentioned that the Recent acmaeiid gastropod *Lottia* Gray (in Sowerby, 1833) is comparable to *Archinacella* in the shape of both the shell and muscle scar. Thus this report follows Yochelson (1988) in placing the archinacellids within the Class Gastropoda.

Helcionellaceans sensu stricto

The genera referred to the Superfamily Helcionellacea that do not belong to the groups discussed above usually have small, typically high cyrto- to gyroconic, and bilaterally symmetrical shells. No genera of the superfamily are known to have distinct muscle scars within their conchs. Even when preservation is excellent, no muscle scars are found on internal molds, except for an unpaired muscle imprint near the apex. The earliest helcionellaceans known from Tommotian and equivalent strata (or even pre-Tommotian Early Cambrian; see Landing et al., 1989) already had a relatively highly convex shell. Thus it is difficult to envision a plan with serial muscle attachments for biomechanical reasons in these high shells.

Runnegar (1978) suggested that the helcionellaceans probably had only one pair of gills and that the primary multiple retractor muscles were bundled. However, the subsequent simplification of an originally metameric plan seems unlikely if the first metameric mollusks appeared later, as proposed above. Runnegar's (1978) phylogenetic reconstruction is probable only for such evolutionary lineages as those of the gastropods and cephalopods. However, a taxonomic grouping of Paleozoic "monoplacophorans" is largely based on a belief in a metameric organization of the soft body, as illustrated by analogy with the muscle scars in Recent species.

By comparison with Recent "monoplacophorans," it would be expected that the apex in helcionellids is anterior, which means that the shell is exogastric. As primitive mollusks with planspirally coiled shells, the animals were most likely untorted (compare Salvini-Plawen, 1980, p. 254). Therefore, the visceral mass was not rotated 180° with respect to the foot, as in gastropods. Consequently, the anus occupied a posterior position (Figure 2). A sinuous extension of the apertural margin (as in *Tichkaella* Geyer, 1986) and a channel-like conduit (as in some species of *Latouchella* Cobbold, 1921) seem to be useful only as a way to remove metabolic or respiratory wastes from the mantle cavity as quickly as possible. The same function is assumed for the tube or snorkel in most species of *Yochelcionella*. These latter species have a planar apertural margin and do not exhibit adaptations for a semi-infaunal life. Those mollusks that live semi-infaunally usually possess a curved apertural margin and are laterally compressed. The only known species of *Yochelcionella* to have these characteristics is *Yochelcionella americana* Runnegar and Pojeta, 1980. The term "snorkel" for the tube of *Yochelcionella* implies a back-and-forth motion of the water current, and should therefore be avoided for species that did not have an infaunal or semi-infaunal mode of life.

For these reasons, the structural features described above were most likely located in a posterior position, as recently assumed by several

authors (e.g., Peel and Yochelson, 1987; Berg-Madsen and Peel, 1987; Peel, 1988). Therefore, most helcionellacean species probably had endogastric shells with the apex directed backward. Based on reconstructions of the animals' water circulation techniques, this orientation has been discussed by Yochelson (1978, 1979) for the shells of *Yochelsonella*, and is also supported by Linsley's laws (Linsley, 1977). The functional implications for a mode of life analogous to scaphopods, as accepted by several authors, are unlikely for morphological reasons. In addition, this model does not contradict the concept of an ancestral posterior and dorsally extended mantle cavity.

Animals with a posterior mantle cavity that was extended toward the apex could hardly have had multiple gills. A lateral mantle cavity is a much better adaption. However, the extension of the mantle cavity in some helcionelliids is partly recognizable by such respiratory structures as ridges inside the shell (e.g., "*Helcionella*" *arguta*, see Robison, 1964, Pl. 92, fig. 15; *Latouchella merino*, see Runnegar and Jell, 1976, Figs. 2, 4, 5, 9D, and Peel, 1991, Fig. 12) or sub-apical grooves on the exterior (e.g., *Tichkaella hamata*, see Geyer, 1986, Pl. 4, figs. 51a, 52c; and *Latouchella* spp. of Peel, 1991, Fig. 13).

Another possible difference between tryblidiaceans and helcionellaceans lies in the construction of the larval shell, and therefore the form of the apical portion. Geyer (1986, Pl. 3, fig. 34 and Fig. 3) figured the apical portion of a *Latouchella* with a preserved mold of a protoconch. The larval conch is spherical; the adjacent portion is tapered like a neck and shows some concentric wrinkles. These wrinkles probably represent internal molds of narrow chambers that were separated by septa. The adjacent teleoconch is initiated by a second change in growth. This part is much wider and usually is the oldest preserved part of the shell. The apex is, therefore, a secondary apex, and is indicated by shallow and wide furrows on each side that continue into shallow and faintly impressed areas on the internal side of the spire (Geyer, 1986, Pl. 3, fig. 35a).

Internal molds in which the apex is set off by septa occur rather frequently and are easily recognizable (e.g., Geyer, 1986, Pl. 2, fig. 24a). Specimens with preserved septa are also known (e.g., "*Helcionella*" *insulcata* Rasetti, 1957, Pl. 112, figs. 12, 14). The slightly broader end of the teleoconch may have been suitable as an insertion point for the pedal musculature and would be analogous to the muscle insertion area of bellerophonitids as demonstrated by Knight (1952, Fig. 10B).

In the Recent *Neopilina galathea* Lemche, 1957, an asymmetrical coiled larval shell is present (Lemche and Wingstrand, 1959). Another specimen of *N. galathea* has a bulb-shaped apex similar to that in a species of *Vema* (McLean, 1979). However, none of the figured specimens of Recent "monoplacophorans" has the apex exactly bilaterally symmetrical, even though the primary shape of the larval portion is not preserved. In addition, bulb-shaped protoconchs are known from several species of the Tryblidiina.

In summary, the helcionellaceans, in the strict sense, differ from Recent "monoplacophorans" not only in their shell morphology but also probably in the orientation of their shell (including the primary orientation of the apex), in the location of the mantle cavity, in the mode of muscle insertion, and thus in the largely nonmetameric organization of the body. The relevant genera are Early to Middle Cambrian in age, with few representatives in the Late Cambrian. This again distinguishes them from the tryblidiaceans and the older "monoplacophorans" sensu Runnegar and Jell (1976). As proposed by Yochelson (1978) and others, this group should be differentiated from the Amphigastropoda as a high-ranked taxon. On the basis of almost the same arguments, Peel (1991) raised the helcionellaceans to a class-level category that he des-

ignated the "Helcionelloida," a proposal that is endorsed herein.

Merismoconchida

Merismoconch shells were raised to the class-level by Yu (1983) and described in detail by Yu (1984, 1987, 1990). However, the "class" probably includes representatives of different systematic groups. The morphology of *Merismoconcha* Yu, 1979, was recently analyzed by Kerber (1988), who concluded that the assumed metameric organization resulted from a secondarily derived reorganization of the shell cavity. Therefore, merismoconchs do not represent a high-level taxon, and *Merismoconcha* itself must be included within the Helcionellacea.

Parastroconchs

The phylogenetic pathway from helcionellaceans to rostroconchs appears to be documented directly by fossils. These species were called "parastroconchs" by Runnegar (1978). Runnegar and Jell (1976, Fig. C9) described *Mellopegma?* sp. as a helcionellacean with a pegma and a restricted muscle field. A shell with even more resemblance to the rostroconchs was figured by Geyer (1986, Pl. 2, fig. 28). However, whether rostroconchs can be derived from the helcionellaceans by direct descent remains questionable. The presumed orientation of the helcionellaceans (Geyer, 1986, Figs. 3-4; Peel and Yochelson, 1987, Fig. 4; Berg-Madsen and Peel, 1987, Fig. 1B) contrasts with the generally accepted reconstruction for rostroconchs, in which the mantle cavity is located anteriorly. However, the rostroconch organization could also be derived from an ancestor with a posterior mantle cavity.

A more complex problem is the morphological modification of the soft parts. As a result of the change of life habit, rostroconch respiration was adapted to semi-infaunal or infaunal niche. Water was used for feeding as well as for respiration. In the primitive ribeiroids, the water entered the shell probably through the anterior gap and exited posteriorly (Pojeta and Runnegar, 1976). In advanced rostroconchs, water currents had to enter and leave through the posterior shell aperture. The shell of technophorids, finally, had two posterior apertures that most probably served as inhalant and exhalant devices (Pojeta and Runnegar, 1976).

The systematic significance of the pegma in some helcionellaceans should not be overemphasized. A specimen of *Latouchella comma* (see Geyer, 1986, Pl. 3, fig. 37) has a dorsally extended snorkel-like lip along the apertural margin that leaves only a narrow gap between the lip and the rest of the shell. Such a gap is interpreted as a pegma that is homologous to the rostroconch pegma (Runnegar, 1983, Fig. 4A). This structure is systematically significant only if it is shared by a modified muscle apparatus as indicated by the terminal muscle scars in *Mellopegma?* sp. of Runnegar (1983) or gen. et sp. nov.? F of Geyer (1986).

Genera of uncertain systematic position

A number of genera that have been placed within the Superfamily Helcionellacea have a rather flat, limpet-shaped shell, usually with a relatively feeble eccentric apex, and faint to clear, roughly concentric ribs. Many of these genera must be regarded as of uncertain systematic position. Some of them possibly represent opercula of unknown taxa; possible opercula include *Aktugaia* Missarzhevsky, 1976 (compare Yochelson 1978, p. 180), and *Pseudomathevia* Shaw, 1956.

Macroscenella Wilson, 1951, has a short and enrolled apical portion that is not exactly bilaterally symmetrical. It resembles some modern genera of cocculinaceans (such as *Cocculina* Dall, 1882, or *Lepetella* Verrill, 1880). Although alternative interpretations of the systematic

affinity of *Macroscenella* have been published, including an interpretation as an chondrophorine float (Yochelson, 1984), its molluscan affinity seems now to be unequivocal (Yochelson, written commun.) and is best regarded as a gastropod.

The genus *Palaeacmaea* Hall and Whitfield, 1872, is based upon *Palaeacmaea typica* Hall and Whitfield, 1872, which is known from a single specimen from the Upper Cambrian Potsdam Sandstone of New York. Earlier concepts of the genus were based upon photographs of the holotype (Knight, 1941, Pl. 2, fig. 4; Shimer and Shrock, 1944, Pl. 175, fig. 4) and subsequent redrawings of the same specimen. However, the type specimen in the New York State Museum, a fragmented external mold, was re-examined by the author. A latex cast shows that the holotype has a comparatively long, laterally compressed apical portion that was not shown in earlier illustrations. Consequently, the concept of *Palaeacmaea* has to be revised, and species previously assigned to the genus have to be grouped elsewhere. In addition, Yochelson and Stanley (1981) suggested that *Palaeacmaea* is not a mollusk, an interpretation rejected herein. However, *Palaeolophacmaea* Donaldson, 1962, has already been identified as a coelenterate (Yochelson and Stanley, 1981), and the Family Palaeacmaeidae cannot be assigned to the Helcionellacea. These interpretations will be evaluated in a future report.

Systematic conclusions

Because the presumed posterolateral mantle cavity of the helcionellids must be regarded as a conservative feature that reflects a very early stage of conchiferan evolution, the peripodal or anterolateral mantle cavity of modern monoplacophorans is most probably a derived character. Thus the tryblidiaceans should not be considered as the stem group of conchiferan radiation.

The Tryblidiida and Bellerophontida seem to have a close resemblance in the organization of the soft body (Runnegar, 1981), and are probably systematically related. The designation "Amphigastropoda" Simroth (*in* Wenz, 1940) is nomenclatorically available for this group. Tryblidiid as well as bellerophontid Amphigastropoda arose from a stock that presumably had a circularly arranged pedal musculature. Because the Tryblidiida are a sister group of the Bellerophontida, their diagnosis has to be emended. The Tryblidiida are regarded herein as having low to high conical shells with circular patterns of fused or discrete muscle insertions. Hypseloconids probably arose independently from this stock and are therefore an adelphotaxon of the Tryblidiacea (Figure 1).

Cephalopods are clearly derived from the hypseloconids. Thus, by a rigid application of consequent phylogenetic classification (even by the technique of ahierarchical categorization [*Ahierarchische Kategorisierung* of Geyer, 1990]), cephalopods do not represent a high-level systematic category, and are best grouped as an order within the Class Amphigastropoda as a holophyletic taxon. Because phenetic change towards that of the cephalopods mirrors major adaptive innovations in organization and a well-integrated adaptive complex ("grade"), cephalopods are traditionally ranked as a class. However, a higher-ranked taxon, as proposed by some authors, cannot be maintained for the reasons discussed, and the Class Cephalopoda has to be grouped within the emended Superclass Cyrtosoma.

Helcionellaceans are characterized by a retractor musculature that obviously was concentrated and inserted in the apical portion of the shell. Helcionellacean taxa represent a geographically widespread but short-lived (Early Cambrian to Late Cambrian) sister group of the Amphigastropoda and therefore require the category of a class, for

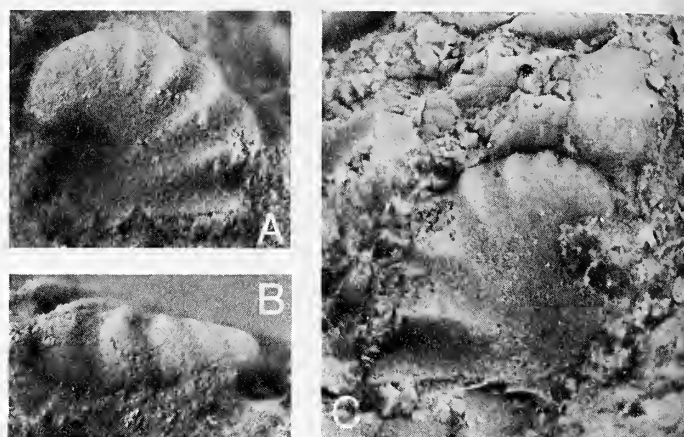


Figure 3. *Latouchella pocatelloensis* n. sp. A, B, Paratype. NYSM 16494, x15; A, Side view. B, Dorsal view. C, Holotype. NYSM 16495. Side view, x15. In the upper right is a pygidium of *Pagetia* sp. Elkhead Limestone, southeast of Pocatello, Bannock County, Idaho.

which the term "Helcionelloconcha" (new) is proposed herein. The Class Gastropoda itself arose unequivocally from the helcionelloconchan lineage by undergoing torsion of the visceral mass with respect to the foot (Figure 1). An alternative systematic concept could group the Order Helcionellida within the Class Gastropoda. However, this would lump torted and untorted mollusks within one class.

Systematic paleontology

Occurrence and age

The mollusks described and figured below were collected from the Middle Cambrian of the Wasatch Mountains or the Bannock Range of Idaho.

The specimens of *Latouchella pocatelloensis* n. sp. and *Protoconchioides douli* n. sp. were collected by John Malinky, University of Maryland, and Robert Livingston from an exposure of the Elkhead Limestone (Trimble and Carr, 1976) located southeast of Pocatello, Bannock County, Idaho. This locality is on the east side of Mink Creek Road, where the northern boundary of Caribou National Forest crosses Mink Creek Road. The outcrop is situated north of an unnamed gravel road that leads east from Mink Creek Road and runs parallel to Kinney Creek (ca. 112° 24' W, 42° 45' 40" N). The fossils were discovered in a layer of fossil wackestone approximately 3.0 m above the base of the exposure.

In addition to the molluscan species described below, abundant trilobite fragments, dominated by *Kootenia* and other members of the Corynexochida and species of the Ptychopariida; rare hyoliths; and articulate brachiopods are the other macrofaunal elements found at that locality. Trimble (1976) cited written communications from A.R. Palmer in 1958, 1961, and 1963 that reported *Ehmaniella* as well as *Ehmania*-, *Solenopleura*-, and *Alokistocare*-like trilobites at the Mink Creek Road locality. Of these taxa, only *Ehmania* can be recognized with certainty in samples used for this study. Other faunal elements will be dealt with in a future paper. The faunas from this locality probably indicate an age within the *Bathyuricus*-*Elrathina* Zone of the Middle Cambrian.

Latouchella arguta (Resser, 1939) was reported from the Langston Formation at the well-known locality of Twomile Canyon ("Two Mile



Figure 4. *Latouchella arguta* (Resser, 1939). USNM 340602 on the same rock piece as the holotype of "*Pagetia* (*Eopagetia*) *resseri* Kobayashi, 1943" (see Resser, 1939, Pl. 2, fig. 8). A, Side view, x10. B, Enlargement of the exterior of the shell showing reticulate ornament, x20. Twomile Canyon southeast of Malad City, Oneida County, Idaho.

Canyon" of Resser, 1939), 3.2 km SE of Malad City, Oneida County, Idaho, on the north side near the mouth of the canyon. Further descriptions of the location and fauna were given by Resser (1939).

Class HELCIONELLOIDA Peel, 1991

Diagnosis.—See Peel (1991, p. 173).

Order HELCIONELLIDA n. order

Diagnosis.—As for the class.

Family HELCIONELLIDAE Wenz, 1938

Genus LATOUCHELLA Cobbold, 1921

Type species.—*Latouchella costata* Cobbold, 1921.

Discussion.—*Oelandia* Westergård, 1936, is believed to be distinct from *Latouchella* in the asymmetrically arranged, offset plicae on the convex (anterior) side of the shell (Peel and Yochelson, 1987; Peel, 1991). However, *Latouchella* is based on *L. costata* Cobbold, 1921. The latter species is known from the Comley quarry, Shropshire, from one conch, which has one side embedded in the sediment. An examination of this specimen seems to prove that *L. costata*, like *Oelandia*, has offset plicae on the convex side of the whorl. Thus the presence of offset plicae is insufficient to distinguish *Oelandia* from *Latouchella*.

A second point to consider is whether or not two species-groupings are recognizable within *Latouchella*. The first group has strongly laterally compressed conchs with rugae with their greatest height laterally, and the second group has a less laterally compressed shell with rugae that traverse the outer side without remarkable flattening. Typical representatives of the first group are *L. costata* Cobbold, 1921; *L. penecyrano* Runnegar and Jell, 1976; *L. comma* Geyer, 1986; and *Oelandia pauciplicata* Westergård, 1936. The second group includes *L. merino* Runnegar and Jell, 1976; *L. accordionata* Runnegar and Jell, 1976; and *L. arguta* n. sp. (described below). An appropriate generic name for this second group could be *Chabaktiella* Missarzhevsky (in Missarzhevsky

and Mambetov, 1981). However, as only one imperfectly preserved specimen of the type species, *C. shabaktensis* (*C. "shabaktensis"* of Missarzhevsky, in Missarzhevsky and Mambetov, 1981), has been figured, the shape of the aperture in conchs of this genus needs further investigation.

A genus with conchs that are morphologically similar to *Latouchella* is *Bemella* Missarzhevsky (in Rozanov et al., 1969). The only feature that differentiates *Bemella* from *Latouchella* is the general shape of the shell; it is a low, laterally compressed dome with the posterior end of the aperture extended very close to the apex. However, based on the smaller conch size of most of the species of *Bemella* and general absence of an extended aperture, *Bemella* species may be regarded as pedomorphic or neotenic after *Latouchella*. However, systematic evaluation of these genera needs additional material and further investigation. One species of this type is *B. parula* Missarzhevsky (in Rozanov et al., 1969). Some of the specimens figured as *Bemella* seem to be juvenile specimens of *Latouchella*. A more important feature than the external gross morphology is probably the internal form of the apex, but it cannot be determined in the majority of species of the two genera.

The monotypic genus *Songlingella* Chen et al., 1981, must be synonymized with *Latouchella*. *Songlingella* strongly resembles larger species of *Latouchella*, such as *L. accordionata* Runnegar and Jell, 1976, and *L. iacobinica* Geyer, 1986, that have rather sharp comarginal rugae and an open spire. *Songlingella* conchs differ in having a conspicuous lateral compression that is typical for smaller species of *Latouchella* with broader ribs. However, this difference is gradational between the genera and does not require generic distinction.

LATOUCHELLA POCATELLOENSIS n. sp.

Figure 3A-C

Diagnosis.—*Latouchella* species with cyrtococonic shell; aperture strongly upturned toward posterior into an extended exhalant channel; ratio of length to width to height about 2/2.2/1; external and internal side similar; with prominent comarginal rugae on the external side of the whorl.

Description.—Shell cyrtococonic, moderately high, laterally compressed. Aperture elliptical. Apertural margin lies essentially in one plane but is strongly bent upward in posterior view to form a conspicuous exhalant channel (Figure 3C). Ratio of height to length to width about 2/2.2/1.

External and internal side similar, both with prominent comarginal rugae. Rugae equidistant and run over the anterior side of the whorl; highest near each side of the midline of the exterior and fade out toward the interior side of the whorl.

Ornament not well-preserved, only faint radial lines visible on the convex side of the whorl.

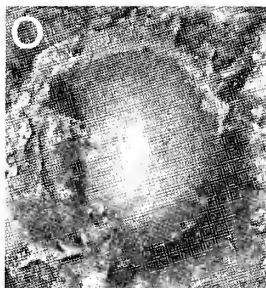
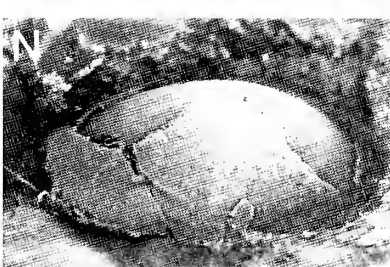
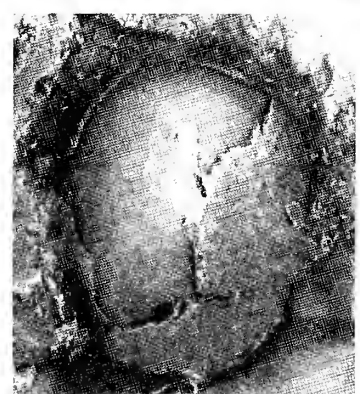
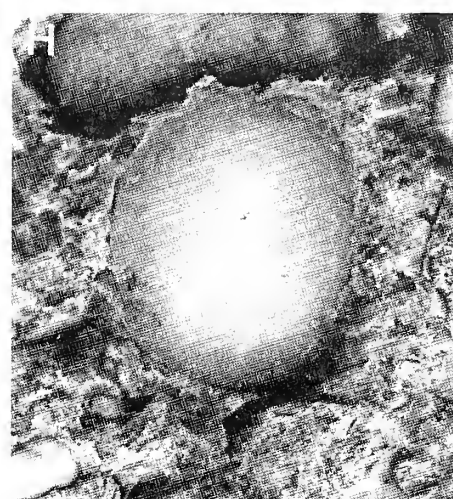
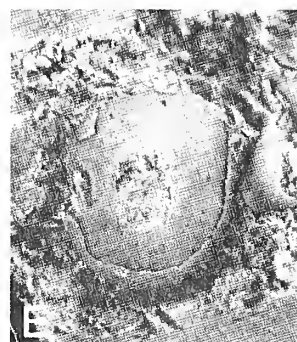
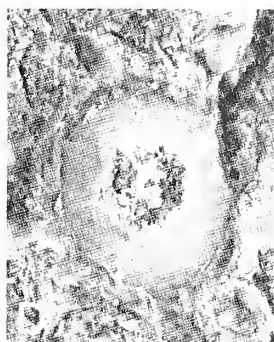
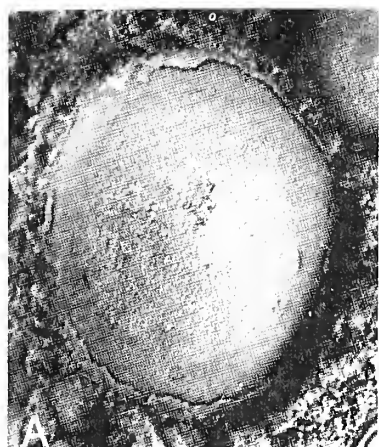
Discussion.—The species is rather similar to *Latouchella arguta* Resser, 1939, from the Wasatch Mountains, and to *L. merino* Runnegar and Jell, 1976, from Australia. It differs from *L. merino* in having a less-extended but more upturned exhalant channel and less-inflated rugae.

The posterior apertural margin in *Latouchella arguta* is bent upward only weakly and is not conspicuously extended in side view. Despite the fact that the only known specimens of *L. pocatelloensis* n. sp. are internal molds, *L. arguta* differs in the comarginal rugae of the shell, which are very broad and much wider than the interrugae depressions on the peripheral side of the shell.

Latouchella burlingi (Resser, 1939) (pro *Helcionella burlingi*



Plate 1. *Protoconchiodes douli* n. sp. Elkhead Limestone, southeast of Pocatello, Bannock County, Idaho. All specimens blackened and subsequently coated with magnesium oxide. All figures x5, except Figure *P* (x10). *A-C*, Holotype, internal mold with patches of shell adhering near the apical margin. NYSM 16496, on the same rock fragment as NYSM 16497 (Plate 1, figure *D*); *A, B*, Dorsal views under different illuminations to show the ring-shaped muscle scar; *C*, Side view. *D*, Paratype, internal mold. NYSM 16497, on the same rock fragment as the holotype (Plate 1, figures *A-C*). Dorsal view. Apical portion not preserved as a result of incomplete fill of the cavity underneath the shell. *E*, Paratype, internal mold with patches of shell adhering near the apical margin. NYSM 16498, on the same rock fragment as NYSM 16499 (not figured) and NYSM 16503 (Plate 1, figures *M, N*); Dorsal view. Apical portion not preserved as a result of incomplete filling of the cavity underneath the shell. *F-H*, Paratype, internal mold. NYSM 16500, on the same rock fragment as NYSM 16504 (Plate 1, figures *O, Q*); *F*, Side view showing the change in profile on the posterior slope; *G*, Frontal view, *H*, Dorsal view with very faint ring-shaped muscle scar and radial riblets posteriorly. *I, K*, Paratype, internal mold with patches of shell adhering near the apical margin and with healed injuries. *I*, NYSM 16501A. Dorsal view with very faint muscle scar and with faint radial riblets. Counterpart of NYSM 16501B (Plate 1, figure *K*). *K*, Paratype, latex cast of exterior of shell with healed injuries. NYSM 16501B. Dorsal view with faint radial riblets. Larger pit partly filled with callus of shell material. Counterpart of NYSM 16501A (Plate 1, figure *I*). *L*, Paratype, latex cast of a partly exfoliated specimen. NYSM 16502, on the same rock fragment as the holotype of *Latouchella pocatelloensis* n. sp. Dorsal view. *M, N*, Paratype, internal mold with largely preserved shell. NYSM 16503, on the same rock fragment as NYSM 16498 (Plate 1, figure *E*) and NYSM 16499 (not figured); *M*, Dorsal view; *N*, Oblique side view. *O, Q*, Paratype, internal mold lateral part folded and crushed at the left side. NYSM 16504, on the same rock fragment as NYSM 16500 (Plate 1, figures *F-H*); *O*, Anterior view; *P*, Anterior view at higher magnification shows the nipple-like apical portion in a complete internal mold x10; *Q*, Dorsal view.



Resser, 1939) from the Langston Formation at Bear River, Idaho, has similar broad comarginal rugae as in *L. arguta*. In addition, it differs from *L. pocatelloensis* n. sp. in dorsal view, according to Resser's (1939) description and figures, in having flattened rather than strongly convex sides on the rugae.

A species similar to *Latouchella pocatelloensis* n. sp., which has the sub-apical portion with a strongly upturned posterior aperture, is *Latouchella holmdalei* Peel, 1988. The latter differs in having obvious folds at the sides of the exhalant channel, a comparatively lower shell, and less convex comarginal rugae.

Another form similar to *Latouchella pocatelloensis* n. sp. was described and figured as "*Helcionella* sp." by Lochman (in Cooper et al., 1954) from the Arroyos Formation of the Caborca area, Sonora, Mexico. The single known specimen came from approximately coeval strata (*Glossopleura*-*Kootenia* Zone). This specimen differs from *L. pocatelloensis* n. sp. in having a relatively wider shell and having an aperture that is upturned posteriorly only weakly.

Size.—Height 1.7 to 2.0 mm, length 2.1 to 2.4 mm, width 0.9 to about 1.1 mm (est.).

Etymology.—Named for the city of Pocatello, Idaho, near the type locality.

Holotype.—The specimen shown in Figure 3C (NYSM 16495).

Material.—Two specimens. NYSM 16494 (paratype, Figure 3A, 3B) and NYSM 16495 (holotype, Figure 3C, on the same rock fragments as the paratype of *Protoconchioides douli* n. sp. on Plate 1, fig. L, and an unfigured paratype of *P. douli*).

LATOUCHELLA ARGUTA (Resser, 1939) emend.

Figure 4A, B

Helcionella arguta RESSER, 1939, p. 23, Pl. 1, figs. 38-41.

"*Helcionella*" *arguta* Resser. ROBISON, 1964, p. 561-562, Pl. 92, figs. 11-13, 14?, 15-17.

Emended Diagnosis.—*Latouchella* species with cyrtconic shell, aperture weakly upturned to posterior; ratio of length to height about 3.5/4.5, external side with strongly prominent, comarginal rugae that run over the convex side of the whorl. Ornamented with fine radial and concentric threads.

Description.—Shell cyrtconic to gyroconic, moderately high, laterally compressed. Aperture slightly subrectangular. Apertural margin lies in essentially one plane, only weakly bent upward posteriorly. Exhalant channel not strongly extended in lateral view. Ratio of length to height to width in larger specimens usually about 3.5/4.5/2.3.

External side with prominent comarginal rugae. Rugae equidistant, extend over the anterior side of the whorl; highest marginal to the anterior of the midline, fade out toward the posterior, concave side of the whorl.

Convex side of the shell covered with a reticulate ornament of fine radial threads and concentric growth lines that intersect at almost right angles. Other parts show only densely spaced growth wrinkles.

Additional features of this species are described by Robison (1964, p. 561). These include the presence of two longitudinal ridges on interior of the posterior side of the shell.

Discussion.—Robison (1964) described and figured material of *Latouchella arguta* from the *Bolaspidea* Zone of the Wheeler and Marjum Formations of the House Range and the Drum Mountains, Utah. The material consists mostly of silicified specimens etched from limestones. It seems, therefore, that smaller specimens that have a more gyroconic shape of the shell were preferentially recovered. However, it is uncertain whether all specimens belong to the same species. As an

example, the shell on Plate 92, figure 14 of Robison (1964) has a much wider apertural angle and smaller comarginal rugae, although it is comparable in size to other specimens, and allometric growth can thus be excluded as a reason for the morphological difference.

The similarity of *Latouchella arguta* to *L. burlingi* (Resser, 1939) from the Langston Formation at Bear River, Idaho, was stressed in the original description (Resser, 1939, p. 24). *Latouchella burlingi* has similarly broad comarginal rugae that are much wider on the peripheral side of the shell than the rather small interspaced depressions. However, it differs from *L. arguta* in dorsal views, which show, according to Resser's (1939, Pl. 1, fig. 42) description and figure, flattened rather than strongly convex sides of the rugae. The differences from *L. pocatelloensis* n. sp. are discussed above.

The Australian species *Latouchella merino* Runnegar and Jell, 1976, differs mainly in the more extended exhalant channel, and in that the relatively narrower, numerous rugae are higher.

Size.—The figured specimen has a height of 3.6 mm and a length of 4.6 mm. The width of approximately 1.9 mm is estimated because the shell is partly embedded. Two specimens in Resser's collection attain a 6 mm height and an 8 mm length. According to the figures of the material, Robison's (1964) specimens reach more than 4.5 mm in height, but the etched specimens are generally smaller.

Material.—One specimen, USNM 340602 (Figure 4A, 4B); on the same slab as the holotype of "*Pagetia* (*Eopagetia*) *resseri* Kobayashi, 1943" (see Resser, 1939, Pl. 2, fig. 8, figured as *Pagetia clytia*; refigured in Kobayashi, 1944, Pl. I, fig. 14 as *Pagetia* (*Eopagetia*) *resseri*). External mold. Type material figured by Resser (1939, Pl. 1, figs. 38-40).

Class AMPHIGASTROPODA Simroth in Wenz, 1940, emend.

Emended diagnosis.—A class of the Subphylum Conchifera characterized by simple, low to high conical, limpet- or low cap-shaped shells with ring-shaped, horseshoe-shaped, or multiple muscle scars arranged in a concentric pattern with respect to the apex.

Order TRYBLIDIIDA Lemche, 1957, emend.

Emended diagnosis.—Amphigastropods characterized by simple, low to high conical, limpet- or low cap-shaped shells with ring-shaped, horseshoe-shaped, or multiple muscle scars arranged in a concentric pattern with respect to the apex.

Suborder HYPSELOCONINA, n. suborder

Diagnosis.—Tryblidiids characterized by simple, low to high conical shells usually with ring-shaped or horseshoe-shaped muscle scars or imprints of the pedal musculature arranged in a simple concentric pattern with respect to the apex. Apex simple, subcentral in position.

Discussion.—As discussed above, the Upper Cambrian to Ordovician genera of the Family Hypseloconidae Knight, 1956, possess morphological features that indicate that they might have been derived from a group that includes *Protoconchioides*, or were descended from the same stem group. Thus this group is raised to the Suborder Hypseloconina, a sister group of the Tryblidiina. The Hypseloconina are characterized by the pedal musculature, which is basically not secondarily split into the serial muscles as in the Tryblidiina. Thus the pedal musculature is usually indicated by circular or horseshoe-shaped muscle imprints.

It should be noted that the discrete multiple muscle imprints in species that are placed within the Hypseloconina (such as *Protoconchioides? rasettii* n. sp.; *Kirengella ayaktchica* Rozov, 1968; or *Lenaella octobinaria* Byalij, 1973) usually form prominences on the

internal shell surface. In contrast, multiple muscle scars in species of the Tryblidiina are usually represented by comparatively deep grooves on the internal side of the shell.

Family PROTOCONCHIOIDIDAE, n. family
Diagnosis.—Hypseloconins characterized by simple, low conical shells with ovate outline, an apertural margin in one plane, and a faint, ring-shaped impression parallel to the margin.

Discussion.—The Family Protoconchioididae n. fam. is based on the genus *Protoconchioides* Shaw, 1962. It is characterized by simple, low conical shells with ovate outline. The apertural margin is in one plane. The internal shell surface shows a faint, ring-shaped impression parallel to the margin that reflects, in most cases, the insertion of the pedal musculature. An exception is the conch of *Protoconchioides? rasettii*, which additionally has pairs of distinct muscle scars. These muscle scars resulted from the advanced concentration of the musculature into discrete bundles (see below). In most of the family's taxa, the muscle scars are situated comparatively close to the apertural margin.

Shaw (1962) referred several species known from poorly preserved specimens to his proposed subgenus *Protoconchioides*. The molluscan affinity of these species can be regarded as equivocal, particularly when it is considered that some mollusk-like remains have been reinterpreted as sclerites from problematical organisms in Early Cambrian fossil assemblages. However, the conchs of *Protoconchioides hermitensis* (Resser 1945), the type species, as well as *P. douli* n. sp., clearly exhibit molluscan features, as described below. In addition, they can easily be excluded from being sclerites by their comparatively large size.

A possible relative from earliest Cambrian strata was described by Zhao et al., 1980, as *Scenella radiata* Yu, 1979. It has a low conical shell with a nearly central apex and a well-defined circular muscle scar (see Zhao et al., 1980, Pl. 3, fig. 1). In contrast to conchs of *Protoconchioides*, the apex is pointed slightly toward the side. The only known specimen is partly covered by relatively thin shell fragments. Single shell layers can be seen as radial spots and have probably erroneously been identified as muscle scars.

Aegides Jiang, 1980, which superficially resembles "*Scenella radiata*," probably represents a taxon of unknown systematic affinity that is not a mollusk. Jiang (1982) reported serial muscle scars in *Aegides places* (A. "*placus*" of Jiang, 1982), but that species has been excluded from the genus by Qian and Bengtson (1989). However, this feature remains to be confirmed, and Qian and Bengtson (1989) regarded the species as a probable operculum.

Simple conical shells with similar appearance are known from the earliest Cambrian of China, but most of them do not show enough details to indicate phylogenetic and thus systematic relationships. Examples include "*Scenella*" *huijingtanensis* Yu, 1979 (with an apical angle of less than 90°); "*Scenella*" *emeishanensis* He, 1980 (in Yin et al., 1980; ovate in outline, with a very faint ring-shaped muscle scar); and "*Tannuella*" *retusa* Jiang, 1982 (with an apical angle of less than 90° and concentric undulations).

Several cap-shaped, patelloid genera are known within the tryblidiacean Family Kirengellidae Starobogatov, 1970; most of them resemble *Protoconchioides* in the shape of the shell. However, all have obvious, often very deep, multiple muscle impressions that indicate a serial pedal muscle. Of these, *Lenaella* Byal'j, 1973, from the Lower Ordovician of the Siberian Platform, is closest morphologically to *Protoconchioides*. It has about seven pairs of densely spaced muscle scars in a regular circle.

Patelliconus Horný, 1963 (non 1961, compare reference; type species *Palaeacmaea primula* Perner, 1903), from the Middle

Ordovician of Bohemia superficially resembles *Protoconchioides* in the general shape of the shell and in the almost circular muscle imprint. However, *Patelliconus* is much larger and has a strongly rugose outer surface, and the muscle scar lies in a more central position.

Superficially similar characters are also known in the archinallid genera *Archinacella* Ulrich and Scofield, 1897, and *Floripatella* Yochelson, 1988. *Archinacella* is similar in its ovate outline and the ring-shaped muscle scar, but it differs clearly from *Protoconchioides* in the comparatively marginal position of the apex, the broader muscle scar, and a non-planar apertural margin. *Floripatella* is easily distinguished by a more circular outline and a nearly central apex. In addition, *Floripatella* has a relatively deep, horseshoe-shaped muscle scar.

PROTOCONCHIOIDES Shaw, 1962, emend.
Type species.—*Scenella hermitensis* Resser, 1945.
Emended diagnosis.—Genus of the Protoconchioididae characterized by a low, conical shell that is ovate in outline; apex subcentral to slightly anterior(?); external surface smooth or with faint concentric undulations; internal surface of shell smooth, with weak circular muscle scar situated about one-fourth to one-third of the way from margin to apex.

Discussion.—See that of Family Protoconchioididae.
Generic synonymy.—Shaw (1962) assigned several mostly poorly preserved species to *Protoconchioides*. These species were *Scenella hermitensis* Resser, 1945, the type species, from the Middle Cambrian Gateway Formation of the Grand Canyon; *Scenella varians* Walcott, 1886, from the Middle Cambrian Parker ("Georgia") Formation of Vermont; *Scenella? conula* Walcott, 1884, from the Middle Cambrian Eldorado Limestone of the Eureka District, Nevada; *Scenella virginica* Resser, 1938, from the Middle Cambrian of the Shady Dolostone of Virginia; and *Scenella (Protoconchioides) palmeri* Shaw, 1962, from the Middle Cambrian Pioche Shale, Eureka District of Nevada.

The major features of these species were listed in a synoptic table by Shaw (1962, Tab. 2). However, some of the measurements of the apical angles (in lateral view) seem to be incorrect, for example in *Protoconchioides conula* (Walcott, 1884), where it is about 100-115°, or in *P. virginica* (Resser, 1938), where it is estimated to be about 95-100°. In addition, *P. palmeri* appears to be a possible junior synonym of *P. conula*, and *P. virginica* is difficult to recognize because of its very poor preservation. *Protoconchioides hermitensis* and *P. palmeri* show a lirate ornament, which also seems to be present on the external surface of conchs of *P. conula* and, possibly, *P. varians*. The internal surfaces of the shells of *P. hermitensis*, *P. virginica*, and *P. conula* possess a ring-shaped muscle scar as in *P. douli* n. sp.

Lochman (in Cooper et al., 1954, Pl. 17, figs. 6-8) figured a specimen as "*Scenella* cf. *S. reticulata*" that appears to be very close to *P. douli* n. sp. of this report. The specimen is slightly higher and somewhat smaller than the specimens of *P. douli* n. sp. described herein and has very faint concentric undulations in addition to the muscle scar. It was found in the Buelna Formation of the Caborca region, Mexico, in the upper part of the *Bonnina-Olenellus* Zone (uppermost Lower Cambrian in the Pacific faunal province).

PROTOCONCHIOIDES DOULI n. sp.
Plate 1

Diagnosis.—Species of *Protoconchioides* with a conch with a length to width ration of 1.19/1.28; longitudinal apical angle 110 to 120°; external surface of the shell almost completely smooth; muscle scar situated at about one-fourth to one-third of the way from margin to apex.

Description.—Shallow conical shells with ovate outline. Apex low, subcentral in position, usually located slightly toward anterior. Apertural margin lies in one plane. Ratio of length to width varies from 1.19 to 1.28, ratio of height to length 0.36/0.41. Longitudinal apical angle 110 to 120°. Shell relatively thin.

External surface almost smooth, rarely with extremely indistinct growth lines. No obvious lirae visible. Surface microscopically rough.

Inner surface almost smooth except for muscle scar and radial riblets and lines. Ring-shaped scar faintly impressed, parallel to the apertural margin, located about one-fourth to one-third of the way from margin to apex. On the holotype, two small pits within the ring-shaped muscle scar may indicate locations of especially firm insertions of muscle bundles (Plate 1, figures A, B). Central parts of the shell (inside the muscle scar) slightly convex on ventral side; slightly convex to planar or slightly concave on lateral parts outside the ring. Apex, if preserved, projects like a nipple. Radial riblets begin near apex, are very faint or absent, up to five visible in the posterior part. Rarely, faint radial lines are visible that probably resulted from the presence of weak radial mantle muscles.

Larval and early growth stages unknown.

One specimen shows two poorly healed injuries (Plate 1, figures I, K). External and internal sides of shell depressions towards the ventral side are visible on both figures. On the dorsal side, at least, the larger pit was partly filled with shell material as a callus-like structure that seems to indicate the individual survived the lesion at least for a certain period.

Discussion.—*Protoconchioides douli* n. sp. differs from other species of the genus in the usually more circular outline of the shell (length to width ratio 1.19/1.28) and a longitudinal apical angle of 110–120°. It differs from most of the other species in the almost completely smooth external surface. For further comparison, see discussion of the Family Protoconchiodidae.

Although preservation is good, no details of the muscle scars are visible. This is due to the small width and the comparatively faint impression of the scars.

Protoconchioides hermitensis (Resser, 1945) from the Middle Cambrian Gateway Formation of the Muav Limestone, Grand Canyon, resembles *P. douli* n. sp. most closely. *Protoconchioides hermitensis* has conchs with a similar size and similar apical angles. Internal molds of *P. hermitensis* conchs yield an elliptical imprint situated at about 35 to 40% of the way from margin to apex. In contrast, *P. hermitensis* conchs can easily be distinguished from those of *P. douli* n. sp. by their external surface, which is covered by fine radial lirae, and their more elongate rather than roundish shape.

Conchs of *Protoconchioides? rasettii* n. sp. are generally comparable to those of *P. douli* n. sp. but differ at least in the presence of distinct pairs of impressions that reflect insertions of a bundled musculature. The pertinent differences in the morphology of the pedal musculature is discussed below under *P.? rasettii* n. sp. However, anteriorly located muscle bundles that resemble those of *P.? rasettii* n. sp. are possibly indicated by small pits in the holotype conch of *P. douli* n. sp. (Plate 1, figures A, B).

Taphonomy.—Most of the specimens examined for this report are preserved as internal molds. The external dorsal surface of the shell is microscopically rough; thus the sediment firmly adheres to the shell. As a result, external features can be seen only by careful preparation.

In a number of specimens, the apex is not preserved, but the apical portion underneath the shell is partly filled with a coarsely crystalline cement (Plate 1, figures D, E). In one specimen, the apical portion of the shell appears to be crushed. After the death of the individuals, the soft parts decayed and the empty shell was buried with the apex up.

Thus the sediment frequently did not fill completely the resulting chamber underneath the shell. Subsequently, the remaining cavity was incompletely filled with sparitic cement or remained free of matrix. In the latter case, the apical portion was occasionally cracked during sediment compaction. A similar taphonomic history has been described by Yochelson (1978) for specimens of his morphologically similar *Floripatella rousseaui*.

Size.—Length from 5.1 to 9.7 mm, width from 4.3 to 7.4 mm, height from 2.0 to 3.5 mm.

Etymology.—From the Chinese word transcribed *dou-li*, the “rain hat”; a reference to the form of the shell.

Holotype.—Specimen on Plate 1, figs. A–C (NYSM 16496).

Material.—Seventeen specimens, including three counterparts. NYSM 16496 (holotype; Plate 1, figs. A–C); NYSM 16497, 16498, 16500–16504 (paratypes; Plate 1, figs. D–M); NYSM 16499, 16505–16508 (paratypes, not illustrated).

PROTOCONCHIOIDES? RASETTII n. sp.

Scenella sp. undet. RASETTI, 1954, p. 59, Pl. 11, figs. 5–8.

Scenella? sp. undet. RASETTI, 1957, p. 968, 969, Table 1.

Scenella sp. KNIGHT AND YOCHELSON, 1960, p. 177, Fig. 46.2

[only]; RUNNEGAR AND POJETA, 1974, Fig. 2; POJETA AND RUNNEGAR, 1976, p. 27, Figs. 7G, 10; RUNNEGAR AND POJETA, 1985, p. 25, Fig. 11.

“*Scenella*” YOCHELSON, 1979, p. 343.

“*Scenella* sp. undet.” GEYER, 1986, p. 72.

Diagnosis.—Species tentatively assigned to *Protoconchioides* with a shell with length to width ratio of 1.15/1.21; external surface of the shell almost completely smooth; muscle furrow situated at about one-fourth of the way from margin to apex, with distinct pairs of impressions that reflect insertions of bundled musculature.

Description and discussion.—Specimens from British Columbia described as “*Scenella* sp. undet.” by Rasetti (1954, Pl. 12, figs. 5–8) are closely related to known *Protoconchioides* species. Although only parts of the external surface of the shell are preserved, the specimens are representatives of an easily recognizable species that is formally erected herein under the name *Protoconchioides? rasettii* n. sp.

Well-preserved internal molds of this species show up to six pairs of small distinct pedal muscle insertions. These small muscle imprints have an elliptical to reniform shape and are superficially serially arranged. The exact pattern has been comprehensively described by Rasetti (1954, p. 60). It should, however, be mentioned that the anteriormost pair of imprints is located slightly in front of a transverse axis that crosses the apex. The result is a comparatively large gap between the muscle scars in the anterior portion of the shell. Because the muscle insertions are grooves on the internal molds, they form prominent hummocks on the internal side of the shell. As earlier shown by Runnegar and Pojeta (1974, 1985), at least most of the pits represent insertion pairs of muscle bundles. A first locus of a comparable type of attachment of muscle bundles in *Protoconchioides douli* n. sp. is indicated by pits on the holotype (Plate 1, figures A, B).

The pits are located in a ring-shaped shallow furrow equivalent to the muscle scars visible in conchs of typical species of *Protoconchioides*. The furrow is parallel to the margin of the shell with a distance of not more than one-fourth of the way from margin to apex. For *P.? rasettii* n. sp., this ring-shaped muscle scar was interpreted as a pallial line by Runnegar and Pojeta (1974, Fig. 2). It must be assumed that the presence of distinct muscle insertions reflects an advanced state of the pedal musculature. Most probably, the ring-shaped furrow no

longer served as an insertion for the pedal musculature. In addition, the furrow is located more marginally than in any of the typical species of *Protoconchioides*. However, the location of the largest muscle scars, just external of the ring-shaped furrow, makes it difficult to accept an interpretation as a pallial line for reasons of functional morphology. It should, however, be mentioned that the lateral cavity has been strongly reduced by comparison with that in *P. douli* n. sp.

In addition to the features described, the internal side of the shell is covered almost entirely by faint, tiny radial lines. These lines most probably reflect weak mantle muscles, as pointed out by Runnegar and Pojeta (1974).

The preserved portions of the shell indicate that the external surface was almost smooth. Obvious lirae are not present.

Etymology.—Named after Franco Rasetti, who first presented a comprehensive description of the specimens.

Types.—Holotype specimen figured by Rasetti (1954, Pl. 12, fig. 5; USNM 123374). Three paratypes deposited under USNM 123375 (Rasetti, 1954, Pl. 12, figs. 6-8). All specimens from upper Mt. Whyte Formation, Mt. Stephen, British Columbia (for additional information see Rasetti, 1954, p. 61).

Acknowledgments

I am indebted principally to J. Malinky for providing the material from the Elkhead Limestone at Pocatello and for improving the language in this report. Special acknowledgments are due to E. Landing for his critical reading and valuable improvements, and to E.L. Yochelson for his constructive criticism. Furthermore, I wish to thank F.J. Collier for the opportunity to study material from the collections of the U.S. National Museum of Natural History and especially for the loan of the specimen of *Latouchella arguta*. Thanks are due finally to E. Berneker, S. Dilling, and H. Schell for helpful comments on the manuscript.

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Three-dimensional graptolites from the upper Middle Ordovician Neuville Formation, Quebec

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Abstract

Limestones of the upper part of the Grondines Member of the upper Middle Ordovician Neuville Formation in the St. Lawrence Lowland of Quebec have yielded a small assemblage of isolated three-dimensionally preserved graptolites. This assemblage includes *Orthograptus ruedemanni*, *O. rivai* n. sp., *Normalograptus mohawkensis*, *Neurograptus margaritatus*, *Climacograptus* (*Diplacanthograptus*) *spiniferus*, *Dicranograptus* sp., and *Pseudoclimacograptus* sp. This assemblage includes the first reported pseudoclimacograptid in eastern North America in the interval spanning the *Corynoides americanus* through *Geniculograptus pygmaeus* Zones, as well as the first known isolated specimens of *O. ruedemanni*, *N.*

mohawkensis, and *Neurograptus margaritatus*.

Specimens of *Orthograptus ruedemanni* commonly occur with another small orthograptid, *O. rivai* n. sp., whose thecal apertures bear paired apertural spines. Morphometric and statistical analyses indicate that *O. rivai* n. sp. is morphologically differentiable from both *O. ruedemanni* and *O. quadrimucronatus micracanthus*, with which it previously has been confused.

Among the synrhabdosomes that form the types of *Orthograptus ruedemanni*, several include specimens of both *O. ruedemanni* and *O. rivai* n. sp., and one includes both of these species as well as a specimen of *Lasiograptus* sp. Thus these synrhabdosome associations are probably taphonomic in origin.

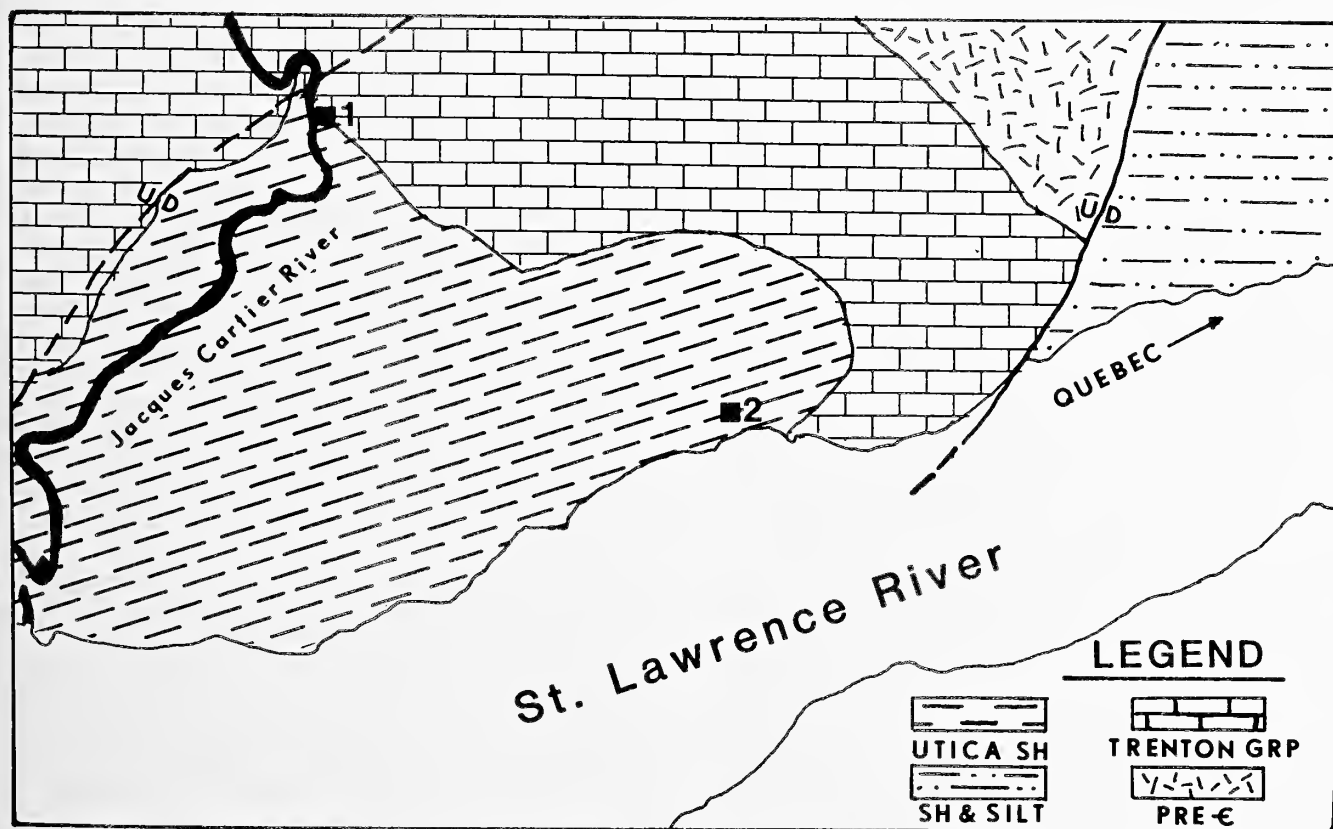


Figure 1. Locality map for the region around Neuville, Quebec. Locality 1 is the left bank of the Jacques Cartier River, 2.4 km south of the village of Pont Rouge. Locality 2 is a road cut behind the L'egare Motel, in Neuville. Adapted from Riva et al. (1977). Scale: 1.0 cm=1.0 km.

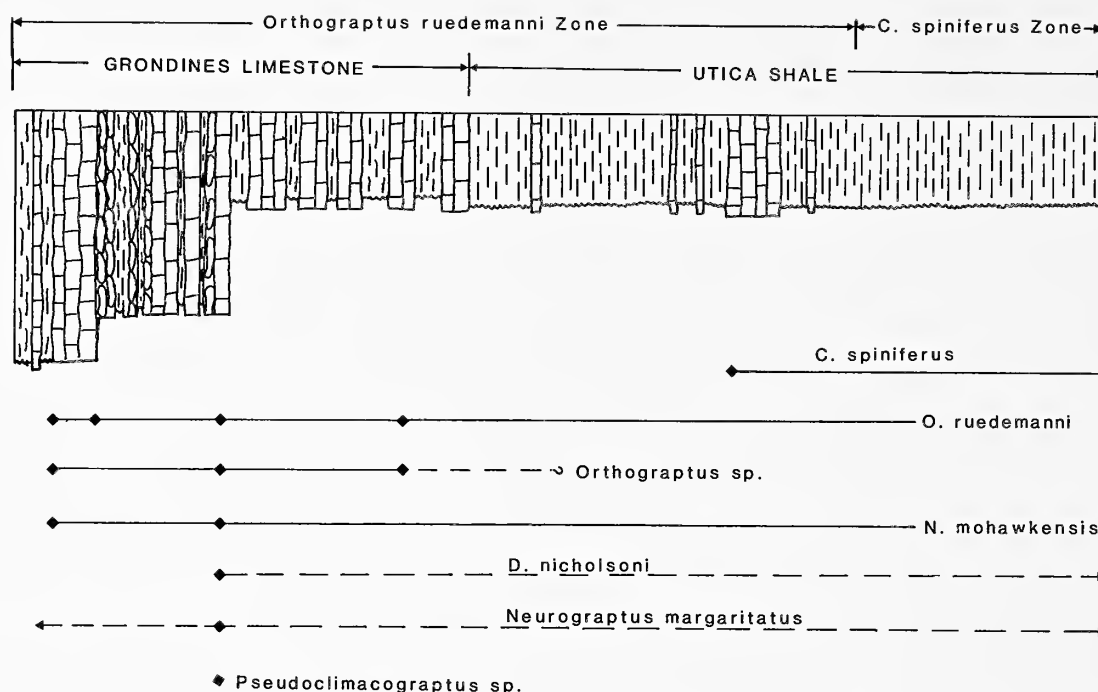


Figure 2. Stratigraphic column of the Jacques Cartier River section. Column illustrates the lithologies and graptolite zonal boundaries present in the upper part of the Grondines Limestone and lower part of the Utica Shale. Diamonds indicate horizons that yield isolated three-dimensional graptolites, solid lines represent graptolite ranges, and dashed lines indicate graptolite ranges inferred from other sections in Quebec and from the Mohawk Valley, New York State. Scale: 11 cm=1.0 m. Adapted from Riva (*in Clark, 1972b*).

Introduction

Three-dimensionally preserved graptolites that can be isolated from their surrounding rock matrix are fairly rare. This is especially true in the upper Middle Ordovician rocks of eastern North America, from which there previously have been no reported occurrences in the interval spanning the *Corynoides americanus* through *Geniculograptus pygmaeus* Zones.

Limestones of the uppermost Grondines Member of the upper Middle Ordovician Neuville Formation crop out on the Jacques Cartier River, 2.4 km south of the town of Pont Rouge, Quebec (Riva, 1969) (Figure 1, Locality 1). These rocks yield a small assemblage of well-preserved unflattened graptolites from several beds within the upper *Orthograptus ruedemanni* Zone. This assemblage includes specimens of *Orthograptus ruedemanni*, *Orthograptus rivai* n. sp., *Normalograptus mohawkensis*, *Neurograptus margaritatus*, *Climacograptus* (*Diplacanthograptus*) *spiniferus*, *Dicranograptus* sp., and *Pseudoclimacograptus* sp.

This assemblage is significant for several reasons. First, our understanding of the morphology of the two key index species to the *Orthograptus ruedemanni* Zone (*O. ruedemanni* and *Normalograptus mohawkensis*) is greatly enhanced by the three-dimensionally preserved material. Second, it represents the first reported occurrence of a pseudoclimacograptid within this interval in eastern North America, as well as the first isolated specimens of several other species. Finally, this occurrence suggests that further detailed collecting in the Neuville Formation and in the lithologically similar and stratigraphically important Dolgeville Formation in New York State may also yield unflattened graptolites.

Stratigraphic setting

The Trenton Group of the St. Lawrence Lowland of Quebec was first subdivided by Clark (1972a) and Clark and Globensky (1973). In the field area near Neuville (Figure 1), the Trenton Group consists of the Pont Rouge, Deschambault, and Neuville Formations (in ascending order). The Neuville Formation is divided into a lower St. Casimir and an upper Grondines Member (Globensky and Jauffred, 1971).

At its type locality on the north shore of the St. Lawrence River near Neuville (approximately 32 km southwest of Quebec City), the Neuville Formation consists of 130 m of thin to thickly bedded limestones (2-25 cm) separated by rare shale beds (Globensky and Jauffred, 1971). The St. Casimir Member consists of 32 m of dark grey, semi-lithographic limestone with extremely rare shale interbeds, and the succeeding Grondines Member comprises 98 m of dark grey, very fine-grained (but rarely semi-lithographic) limestone beds up to 25 cm thick separated by shale interbeds up to 15 cm thick (Globensky, *in Clark, 1972b*).

The contact between the Neuville Formation and the overlying Utica Shale is gradational in outcrops along the Jacques Cartier River 8 km northwest of Neuville (Riva, 1969, p. 528, fig. 7a), as well as at Neuville and at several other exposures in the northeastern part of the Lowland. Elsewhere in the Lowland, however, a disconformity separates the Trenton Group from the Utica Shale. This unconformity becomes younger towards Montreal, where the hiatus spans at least one entire graptolite zone (the *Climacograptus* (*D.*) *spiniferus* Zone) (Riva, *in Clark, 1972b*, p. 51-52, fig. 16).

On the left bank of the Jacques Cartier River 2.4 km south of Pont Rouge, the Grondines Limestone is discontinuously exposed up to its

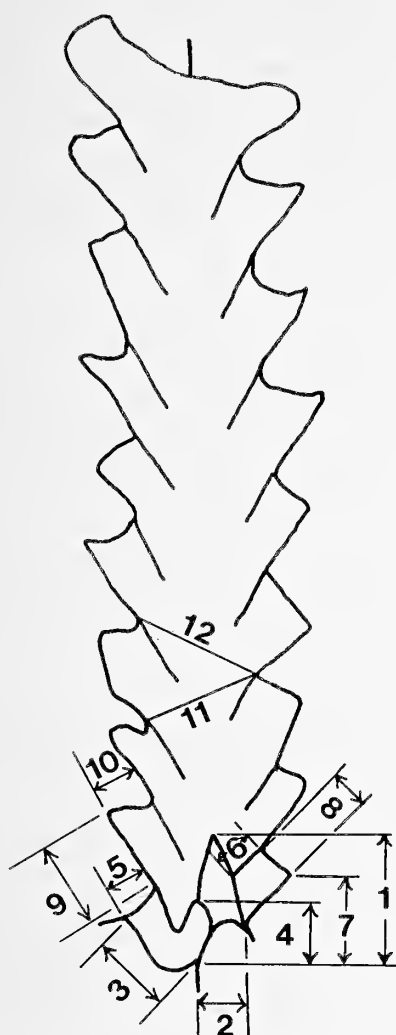


Figure 3. Morphometric analysis of *Orthograptus* species. Illustration of the measurements taken on specimens of species of *Orthograptus* collected in this study: (1) Height of the visible sicula in the obverse view (HVS), (2) Width of the sicula aperture (WSA), (3) Length of Th1 (LTh1), (4) Height of Th1 crossing canal (HTh1CC), (5) Width Th1 aperture (WTh1A), (6) Length of Th2 in the obverse view (LTh2), (7) Height of Th2 above rhabdosome base (HTh2), (8) Width Th2 aperture (WTh2A), (9) Height of each successive theca (HThN), (10) Width of each successive thecal aperture (WThN), (11) and (12) Inter-aperture widths (RW1, RW2, etc.) taken between every two thecae.

contact with the overlying Utica Shale. A small landslide, just downstream and across the river from an old power station, has nicely exposed this contact. Isolated graptolites were obtained from several limestone beds in the Grondines Member, with the bulk of the assemblage coming from 3.0 and 5.0 m below the contact with the Utica Shale (Figure 2). Comparative flattened material was collected here and at Neuville (Figure 1, Locality 2) from the interbedded shales of the upper Neuville Formation and from the shales of the lowermost part of the overlying Utica Shale. A complete description of the graptolite faunas and biostratigraphy of the upper Middle Ordovician rocks of the St. Lawrence Lowland of Quebec can be found in Riva (1969, 1974).

Morphometric and statistical analyses

In nearly all of our collections (isolated and flattened material), *Orthograptus ruedemanni* occurs with another small orthograptid, *O. rivai* n. sp., the thecae of which bear paired apertural spines. In order to evaluate the morphologic differences between these two species, as well as their relationship to *O. quadrimucronatus*, four groups of specimens were subjected to a detailed morphometric and statistical analysis. The four groups consisted of isolated and flattened *O. ruedemanni*, flattened *O. quadrimucronatus micracanthus*, and isolated specimens of *O. rivai* n. sp.

Twenty-one different measurements were taken on each specimen (see Table 1 for a list of measurements taken, mean population values, and standard deviations, and Figure 3 for an illustration of these measurements). One of these measurements requires additional explanation. In all cases in this study, rhabdosomal widths are recorded from a straight line that connects the point of contact of a thecal aperture and its adjacent interthecal septum with that same point on the next theca on the opposite side of the rhabdosome (Figure 3, no. 11- 12). To avoid confusion, this measure of rhabdosome width is referred to as "inter-aperture width." This measurement was taken for every thecal pair, and crisscrosses the rhabdosome from th1¹ to th1², from th1² to th2¹, etc. This method for measuring widths is less affected by flattening and oblique compression than traditional methods, and thus allows for better comparisons between three-dimensional and flattened material. These measurements tend to be less subjective and more reproducible than measurements taken from apertural lip to apertural lip, because apertures are easily distorted and often partially obscured in flattened specimens. However, caution is urged in making unqualified comparisons between the inter-aperture widths reported herein and rhabdosome widths published elsewhere.

VARIABLE	GROUP A		GROUP B		GROUP C		GROUP D	
	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
HVS	0.99	0.12	0.79	0.12	1.21	0.14	0.97	0.12
WSA	0.35	0.04	0.33	0.03	0.44	0.05	0.39	0.05
HGT Th1 ¹	0.50	0.05	0.52	0.08	0.82	0.08	0.65	0.06
Th1 ¹ CC	0.56	0.07	0.52	0.11	0.68	0.08	0.57	0.04
WD Th1 ¹ Ap	0.23	0.04	0.20	0.04	0.31	0.06	0.30	0.06
L Th1 ² Ob	0.18	0.05	0.21	0.06	0.30	0.06	0.23	0.03
HGT Th1 ²	0.54	0.06	0.59	0.07	0.72	0.12	0.60	0.05
WD Th1 ² Ap	0.27	0.03	0.28	0.04	0.34	0.04	0.28	0.05
WD Th2 ¹ Ap	0.28	0.04	0.25	0.04	0.33	0.05	0.32	0.07
HGT Th2 ¹	0.53	0.05	0.55	0.06	0.52	0.08	0.53	0.08
WD Th2 ² Ap	0.27	0.04	0.26	0.03	0.36	0.07	0.32	0.06
HGT Th2 ²	0.43	0.06	0.42	0.06	0.41	0.10	0.40	0.12
WD Th3 ¹ Ap	0.28	0.04	0.25	0.02	0.39	0.06	0.39	0.08
HGT Th3 ¹	0.47	0.07	0.46	0.06	0.56	0.16	0.59	0.09
WD Th3 ² Ap	0.29	0.05	0.29	0.04	0.39	0.05	0.32	0.04
HGT Th3 ²	0.53	0.08	0.47	0.06	0.59	0.11	0.60	0.08
RW 1	0.79	0.10	0.81	0.08	1.10	0.09	0.79	0.04
RW 2	0.86	0.10	0.85	0.09	1.11	0.14	0.82	0.08
RW 3	0.83	0.10	0.87	0.09	1.08	0.16	0.80	0.11
RW 4	0.94	0.13	0.91	0.09	1.21	0.16	0.90	0.16
RW 5	0.88	0.10	0.86	0.08	1.07	0.15	0.79	0.10

Table 1. Group means and standard deviations. Descriptive statistics for twenty-one measured variables on specimens of species of *Orthograptus*. Variable abbreviations correspond to the measurements displayed and explained in Figure 3. Group A is three-dimensional *O. rivai* n. sp., Group B is three-dimensional *O. ruedemanni*, Group C is flattened *O. quadrimucronatus micracanthus*, and Group D is flattened *O. ruedemanni*. All measurements in millimeters.

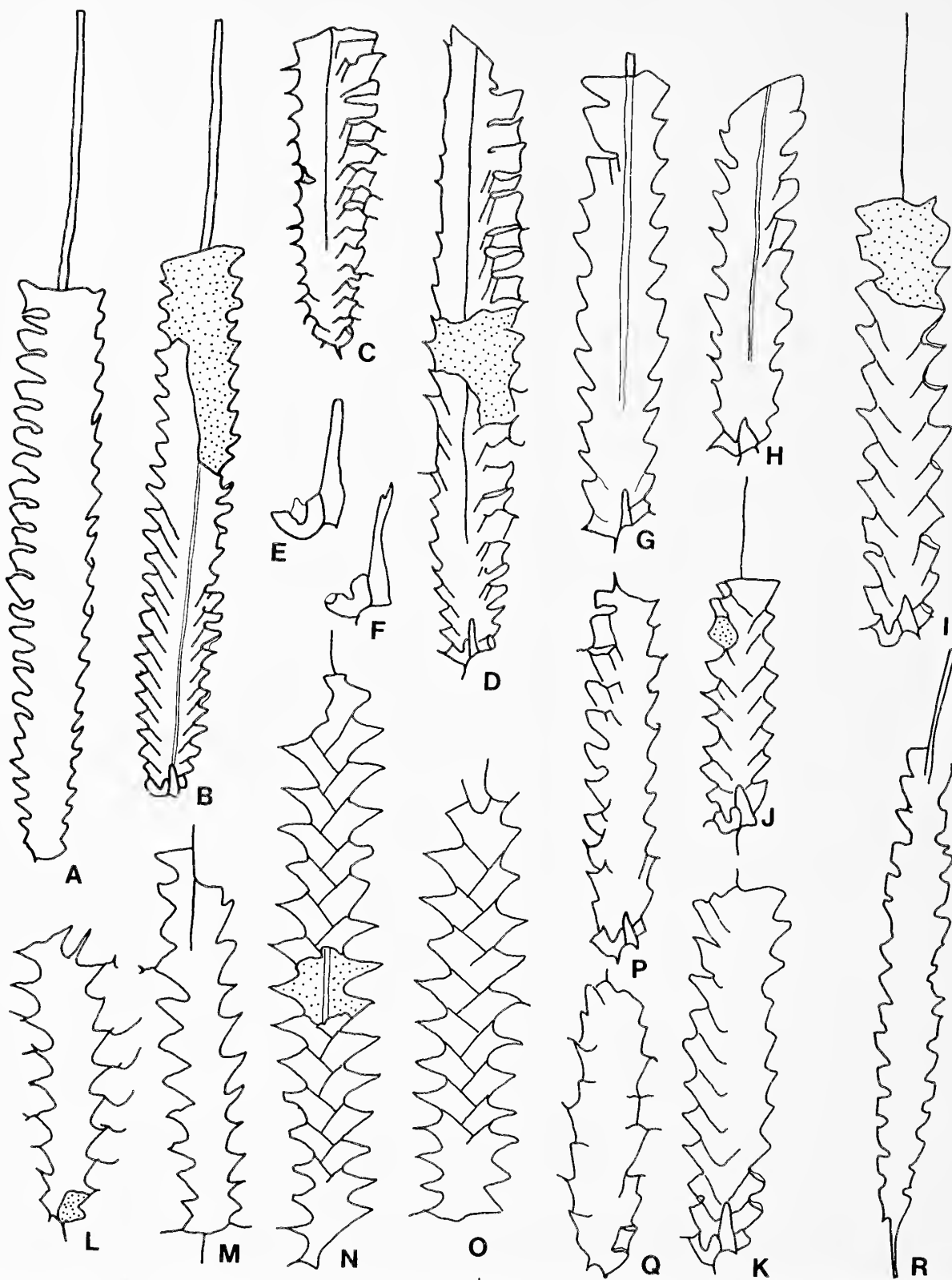


Figure 4. Flattened graptolites. A-D, *Orthograptus quadrimucronatus micracanthus* (ROM 4627-4630) from the lower part of the Utica Shale at Neuville (Locality 2). Lower *Climacograptus spiniferus* Zone (x7). E-K, *Orthograptus ruedemanni*; E-H, (ROM 4631-4634) from the shale interbeds in the upper part of the Grondines Limestone at Locality 1 (Figure 1); I, K, from the Lozo-Joseph 2 core, southern Quebec, 2505 and 2165 feet respectively (on loan from Dr. John Riva); J, (NYSM 16174) from the lower part of the Utica Shale on Chuctanunda Creek, near Minaville, New York State. All *Orthograptus ruedemanni* Zone specimens (x11, except E and F x18). L-O, *Neurograptus margaritatus* (ROM 4635-4638) from the lower part of the Utica Shale at Neuville. Lower *Climacograptus* (D.) *spiniferus* Zone (x11). P-O, *Orthograptus rivai* n. sp.; P, (ROM 4639) from the shale interbeds in the upper part of the Grondines Limestone at Locality 1; O, (NYSM 16175) from the lower part of the Utica Shale on Chuctanunda Creek (same slab as J). Note the spinose apertures. All specimens from the *Orthograptus ruedemanni* Zone (x11); R, Holotype of *Normalograptus mohawkensis*, from Swartztown Creek, near Amsterdam, New York (NYSM 10365), (x9).

These morphometric data were used in a multiple discriminant analysis in order to evaluate the differences among orthograptid species. Multiple discriminant analysis "best separates" groups by using a sequence of linear combinations of variables (Bookstein et al., 1985), and provides an economical means to represent total morphologic distance between populations. The statistical program SPSS-PC was used to perform all of the statistical analyses. The raw data are not included here but are available upon request.

Systematic paleontology

Suborder VIRGELLINA Fortey and Cooper, 1986
Superfamily DIPLOGRAPTACEA Lapworth, 1873, emend. Mitchell, 1987
Family ORTHOGRAPTIDAE Mitchell, 1987
Subfamily ORTHOGRAPTINAE Mitchell, 1987
Genus ORTHOGRAPTUS Lapworth, 1873
Type species.—*Graptolithus quadrimucronatus* Hall, 1865.

ORTHOGRAPTUS RUEDEMANNI (Gurley, 1896)
Plate 1, figures A-I; Plate 3, figure C; Figures 4 E-K, 5, 6

Diplograptus pristiniiformis Hall. RUEDEMANN, 1895a, pp. 453, 455, figs. 2, 3.
Diplograptus ruedemanni Gurley (nomen nudem). RUEDEMANN, 1895b, p. 221, Pl. 1, figs. 2-4, 6, 7, 10; Pl. 2, figs. 1-4; Pl. 5.
Diplograptus ruedemanni GURLEY, 1896, pp. 298, 307.
Glossograptus? eucharis (Hall). RUEDEMANN, 1908, pp. 397-400, Pl. 26, fig. 18, not fig. 19; Pl. 27, figs. 11, 12, not fig. 13; figs. 349, 350, 352; not figs. 346, 347, 348, 351.
Lasiograptus eucharis (Hall). RUEDEMANN, 1934, p. 122, Pl. 15, fig. 17.
Lasiograptus (Thysanograptus) eucharis (Hall). RUEDEMANN, 1947, pp. 461-462, Pl. 81, fig. 33; Pl. 82, figs. 2, 5, 6, 8, 12-20, not figs. 1, 3, 4, 7, 9-11, 21-26.
Orthograptus ruedemanni (Gurley). RIVA, 1969, p. 521, figs. 3f, g; WALTERS, 1977, pp. 941, 946-947, Pl. 2, figs. a-c, e, g, j.
not *Orthograptus ruedemanni* (Gurley). FINNEY, 1986, p. 446, fig. 12h.

Type material.—The lectotype is redefined as an individual (NYSM 16172) within the synrhabdosome NYSM 4913; paralectotypes are NYSM 4914-4922.

Other material.—Twenty isolated three-dimensionally preserved specimens and over fifty flattened specimens. Additional comparative material from the Lozo-Joseph 2 core, southwestern Quebec (on loan from Dr. John Riva, Laval University), and from the lower Utica Shale on Chuctanunda Creek, near Minaville, New York State.

Emended diagnosis.—Species of *Orthograptus* with short rhabdosomes (<13 mm), narrow (maximum 1.3 mm), parallel sided, aseptate; thecae orthograptid, th1¹ with apertural spine, th1² with sub-apertural spine, other thecae nonspinose; proximal end development characterized by pattern G primordial astogeny.

Description.—Inter-apertural widths increase from 0.7 to 0.9 mm at the first thecal pair to 1.0 to 1.25 mm distally (summary of morphometric data is presented in Table 1); generally parallel-sided after the sixth thecal pair. Most specimens less than 10 mm long, with a maximum length of 13 mm and nineteen thecal pairs recorded for one flattened specimen (Plate 3, fig. C). Thecae orthograptid, densely packed, numbering eight to nine in the first 5 mm. Th1¹ bears an apertural spine, th1² a sub-apertural spine, and the remaining thecae are non-spinose.

The proximal-end development is a typical Pattern G primordial astogeny (Mitchell, 1987). The sicula is long and slender (mean length is 1.46 mm) and bears a virgella and two anti-virgellar spines. The mean width of the sicular aperture is 0.36 mm. The sicula remains visible on the obverse side of the colony for an average length of 0.88 mm before it is enclosed by the third thecal pair.

Th1¹ buds from the sicula on the reverse side and grows downward across the virgella onto the obverse side. Below the sicula aperture, th1¹ turns up and outward from the sicula in a broad U. The metatheca of th1¹ is separated from its protheca (and from the sicula) by a large gap (Figure 4E-F and I-K), which is later filled by the protheca of th2¹. The th1 crossing canal grows diagonally downward across the sicula in the form of a hood that is free of the sicula on its ventral (proximal) side and fuses with an upward growing flange. This fusion produces the metatheca of th1² and the foramen from which th2¹ develops. Thus th1² and th2¹ form an asymmetric pair with their prothecae connected in a smooth arch across the reverse side of the sicula (see Mitchell, 1987, for a complete discussion of Pattern G astogeny).

Discussion.—Walters (1977, p. 947) noted that the type specimens of *Orthograptus ruedemanni* (NYSM 4913-4922) are found in association with another small orthograptid (herein referred to as *O. rivai* n. sp.) that possesses thecae with paired apertural spines. Re-examination of this material confirms Walter's observation. Furthermore, *O. rivai* n. sp. even appears with *O. ruedemanni* in the synrhabdosomes that characterize most of the type material (Figures 5 and 6, NYSM 4913 and 4920 respectively). This association also occurs in our isolated three-dimensional material from the Grondines Member, as well as in our collections from outcrops of the lower part of the Utica Shale along Chuctanunda Creek near Minaville, New York.

In order to determine if paired thecal spines are a polymorphic character in *Orthograptus ruedemanni* or if two distinct morphologic variants are represented, the morphometric data gathered from four groups of specimens were compared by the use of both univariate and multivariate techniques. The four groups are (1) isolated three-dimensional specimens of *O. ruedemanni* (non-spinose), (2) isolated three-dimensional specimens of *O. rivai* n. sp., (3) flattened specimens of *O. ruedemanni*, (4) flattened specimens of *O. quadrimucronatus micracanthus*.

Specimens of *Orthograptus quadrimucronatus micracanthus* (Figure 4A-D) are much wider than both the specimens of *O. ruedemanni* and *O. rivai* n. sp. They also continue to widen for a longer interval of colony growth (Figure 7). Additionally, specimens of *O. quadrimucronatus micracanthus* are septate, in contrast to the aseptate rhabdosomes of *O. ruedemanni*. However, rhabdosomal width does not distinguish *O. ruedemanni* from *O. rivai* n. sp., which is also aseptate (Figure 7).

Multiple discriminant analysis was used to evaluate the variables that best distinguish all four groups and to see if individual specimens could be correctly grouped on the basis of the discriminant functions created by the analysis. The analysis generated three discriminant functions that together account for 100% of the total variance. The variable coefficients for each function are listed in Table 2.

Function 1 best discriminates flattened specimens of *Orthograptus ruedemanni* and *O. quadrimucronatus micracanthus* from the isolated three-dimensional material and from each other (Figure 8A). The variables that contribute most to this overall function are inter-apertural widths (especially the width at the first thecal pair, RW 1), the maximum upward growth of th1¹ (HGT Th1¹), the maximum upward growth of th1² (HGT Th1²), and the length of th1² visible in the obverse view (L Th1²). The importance of the contribution of each

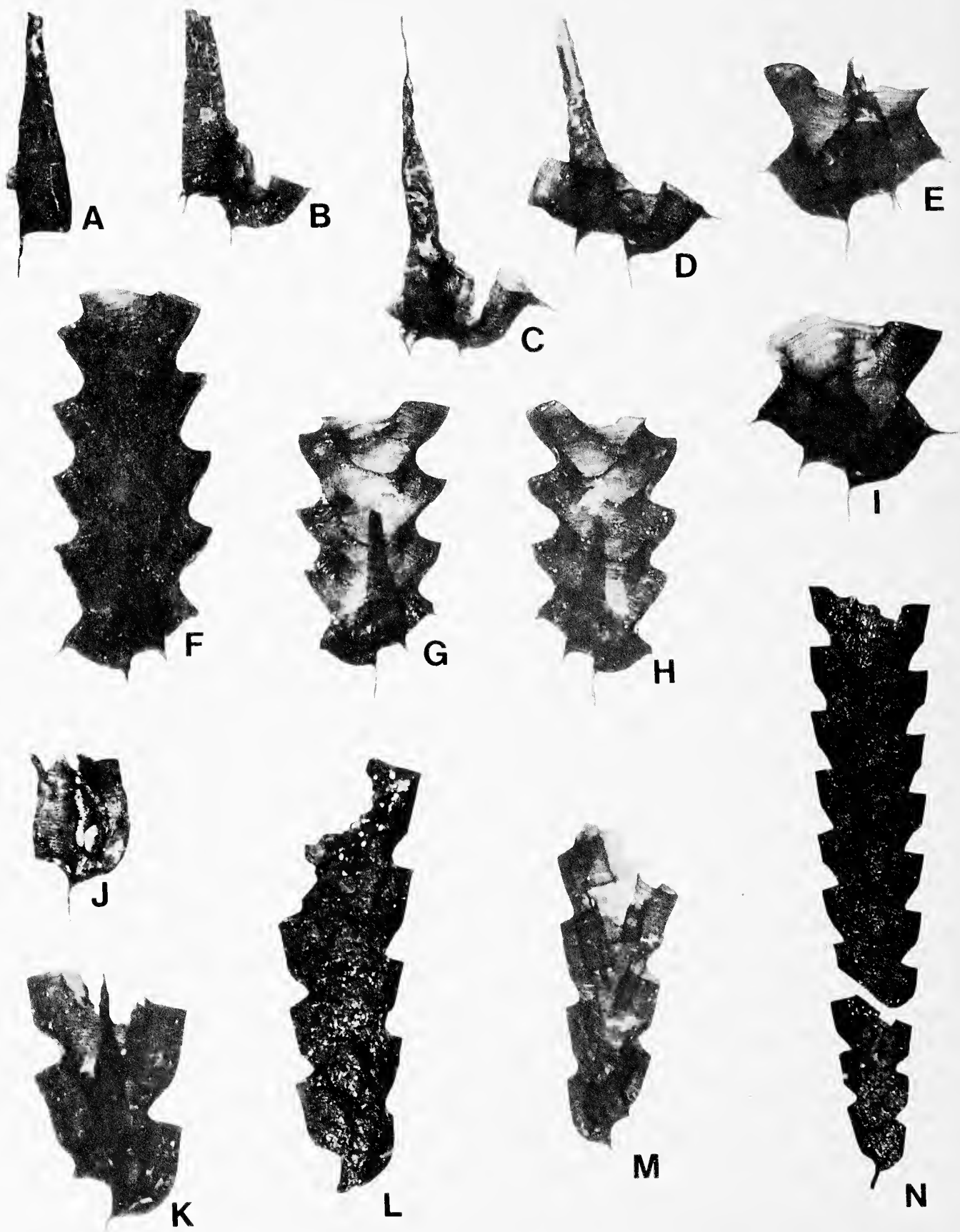


Plate 1. Isolated three-dimensional graptolites. *A-I, Orthograptus ruedemanni*; *A-D*, ROM 4607-4610 (x34); *E, I*, obverse and reverse views of ROM 4611 (x34); *F*, ROM 4612 (x21); *G, H*, obverse and reverse views of ROM 4613 (x21). *J-N, Normalograptus mohawkensis* (ROM 4616-4620); *J, K*, (x34); *L*, (x25); *M*, (x21); *N*, (x15). Note insertion of median septum at the base of the 6th thecal pair. All specimens from 2.5 m in the measured section at Locality 1.

variable is indicated by the absolute value of the function coefficient (Table 2) and by the pooled within-groups correlations between the discriminating variables and the canonical discriminant functions. Three-dimensional specimens of *O. ruedemanni* and *O. rivai* n. sp. are not distinguishable based on Function 1.

Function 2 also separates flattened *Orthograptus quadrimucronatus micracanthus* from the other three groups. The most important contributions to this function come from variables that describe thecal lengths and widths, rhabdosomal widths, and the maximum upward growth of $Th1^1$. Function 2 also does not discriminate between *O. ruedemanni* and *O. rivai* n. sp.

The samples of three-dimensionally preserved *Orthograptus ruedemanni* and *O. rivai* n. sp. are, however, separated by Function 3 (Figure 8B). The primary contribution to this function comes from the height of the visible sicula in the obverse view (HVS, Figure 3). In order to remove the effects of the flattened specimens from the construction of Function 3, a second analysis was run that used only the isolated three-dimensional specimens of *O. ruedemanni* and *O. rivai* n. sp. The two forms were again separated on the basis of length of the visible portion of their sicula. The null hypothesis — that the group means for this character are not significantly different — is rejected at a 99.5% confidence interval ($\alpha = 0.005$) using an F test ($F_{0.005} = 11.4 < F = 12.83$, with

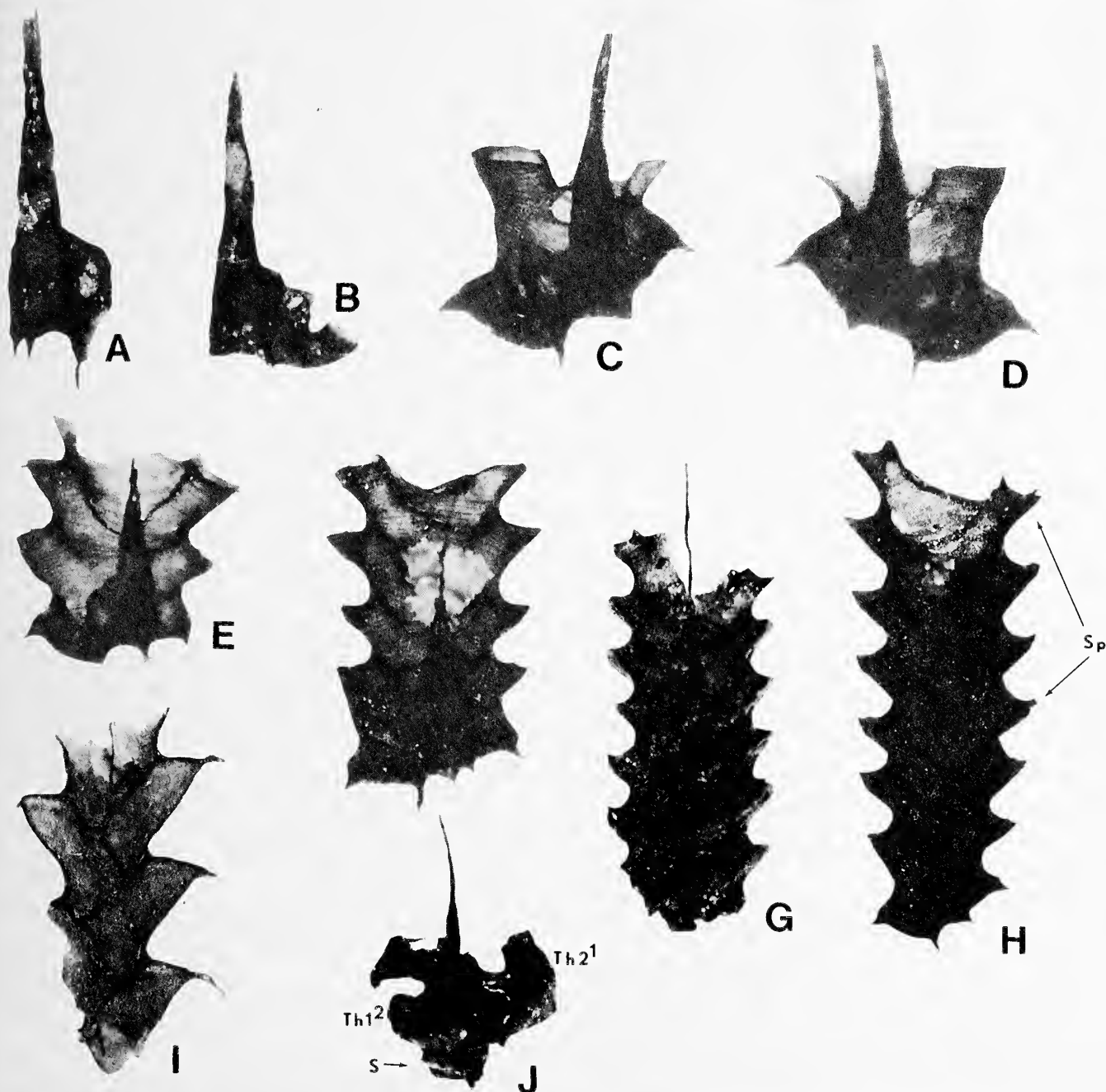


Plate 2. Isolated three-dimensional graptolites. A-H, *Orthograptus rivai* n. sp.; A, B, paratypes ROM 4584-4585 (x34); C, D, obverse and reverse views of ROM 4586 (x34); E, F, paratypes ROM 4588-4589 (x21); G, paratype ROM 4590 (x18); H, Holotype ROM 4583 (x18). Note apertural spines (labeled as Sp). From 0.5 m at Locality 1. I, *Neurograptus margaritatus* (x21), from 2.5 m at Locality 1, ROM 4621. J, *Pseudoclimacograptus* (*Pseudoclimacograptus*) sp., ROM 4622 (x34). Note that $Th1^1$ and the base of $Th1^2$ are torn away, (S=sicula). From 2.5 m at Locality 1.

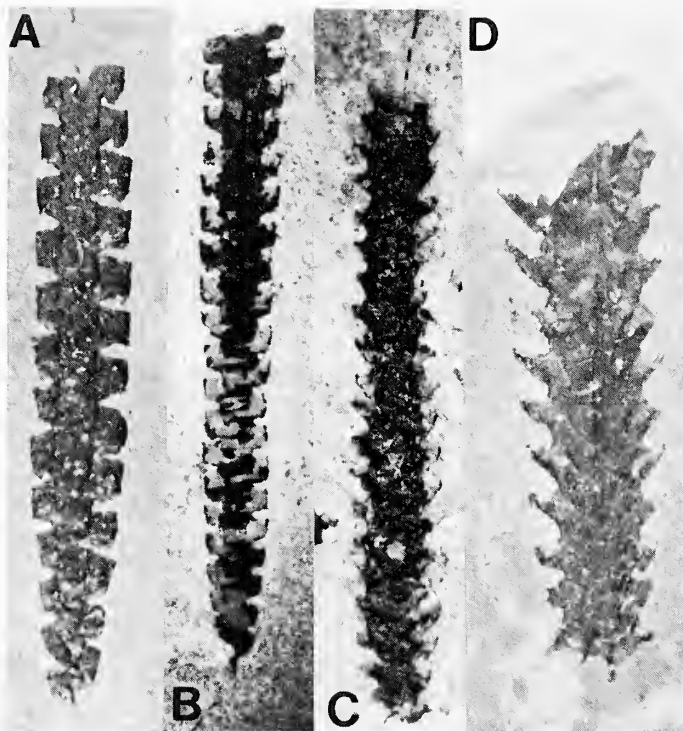


Plate 3. Flattened graptolites. A, B, *Normalograptus mohawkensis* (ROM 4623-4624); A, (x9). Note that there is no median septum. B, Note insertion of median septum at the base of the 11th thecal pair (x6). C, *Orthograptus ruedemanni* (ROM 4625), an exceptionally long specimen. Note the parallel-sided rhabdosome. D, *Orthograptus quadrimucronatus micracanthus* (ROM 4626). Note the rapidly widening, septate rhabdosome (x9). Specimen A from Locality 1, B-D from Locality 2.

1 and 24 degrees of freedom).

To test the validity of these discriminant functions, each specimen was then reclassified into one of the four groups by use of the discriminating functions. Specimens of *Orthograptus ruedemanni* (flat and isolated) and *O. quadrimucronatus micracanthus* were correctly reclassified 100% of the time, and the isolated three-dimensionally preserved specimens of *O. rivai* n. sp. were correctly reclassified in eighteen out of twenty cases, or 90% of the time. 92.3% of total cases were correctly reclassified.

Another variable that distinguishes *Orthograptus ruedemanni* from *O. rivai* n. sp. is the angle of inclination of $th1^1$ to the rhabdosome. The mean angle of inclination of $th1^1$ to the rhabdosome is 41.4° in *O. rivai* n. sp., as opposed to 34.6° in *O. ruedemanni*. This larger angle of inclination produces a blunter proximal end in *O. rivai* n. sp. This variable was not used in the multiple discriminant analyses because angular measurements (calculated from ratios) have different properties of variance than do scalar measurements.

The variation between *Orthograptus ruedemanni* and *O. rivai* n. sp. is significant and permits their recognition as separate biological entities. Given the close overall similarity between this spinose form and typical *O. ruedemanni*, it is conceivable that they were members of a single dimorphic species. However, this interpretation is contradicted by the variable proportions in which these two morphs occur among our collections. In the Jacques Cartier River sample from 2.5 m, *O. ruedemanni* constitutes 100% of the isolated rhabdosomes, whereas at 0.5 m it makes up only 10%. These and other collections demonstrate that

these forms exhibit no regularity in their relative abundance. Thus it is unlikely that they could have been members of the same species.

The presence or absence of paired apertural spines, the difference in the angle of inclination of $th1^1$ to the rhabdosome (characters not used in these quantitative analyses), and the difference in the timing of sicular enclosure within the rhabdosome make them readily distinguishable in well-preserved material. Additionally, the latter two differences represent a meaningful difference in the architecture of the proximal end. Finally, because this variation does not represent geographic variation, the morphologic differences between these two orthograptids indicate that they represent two separate species.

Although Walters (1977) designated NYSM 4913 as the lectotype of *Orthograptus ruedemanni*, he did not indicate a specific rhabdosome within the synrhabdosome on that slab. Because both *O. ruedemanni* and *O. rivai* n. sp. are present in that synrhabdosome, it is proposed herein that the lectotype be restricted to the individual figured as Figure 5C, and labeled on that slab (NYSM 16172).

The presence of two separate species within individual synrhabdosomes indicates that synrhabdosomes are a taphonomic, rather than an astogenetic, phenomenon. This conclusion is supported by the presence of a single specimen of *Lasiograptus* sp. in a synrhabdosome with *Orthograptus rivai* n. sp. and possibly *O. ruedemanni* on the type slab NYSM 4920 (Figure 6). Riva (*in* Clark, 1972b) also noted synrhabdosomes that included two separate genera (*O. quadrimucronatus micracanthus* and *Normalograptus mohawkensis*) in his collections from the

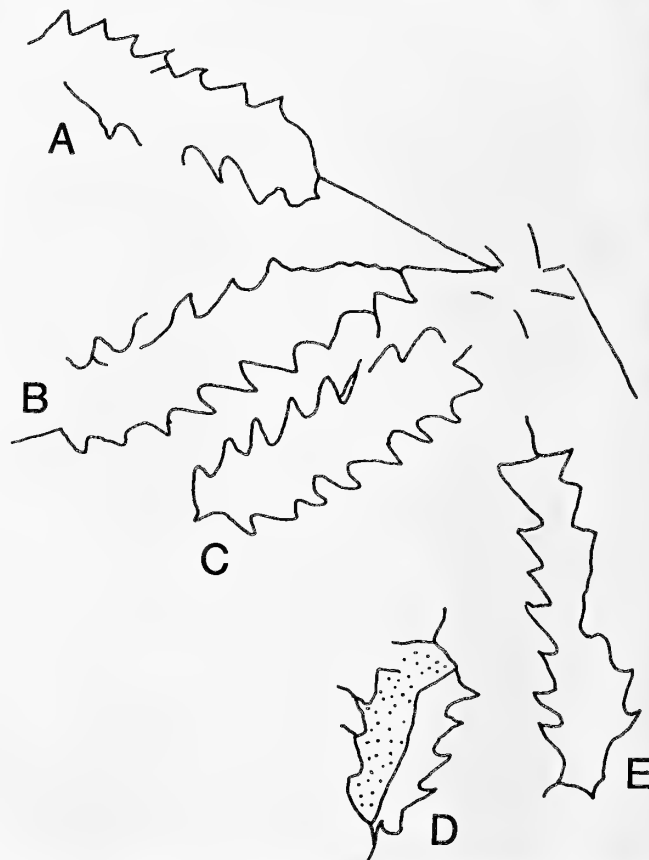


Figure 5. Lectotype of *Orthograptus ruedemanni*. NYSM 4913. Synrhabdosome designated by Walters (1977) as the lectotype for *O. ruedemanni*. Note that specimens B and D have spinose apertures and are *O. rivai* n. sp. Lectotype is here restricted to specimen C (NYSM 16172), which is the best preserved specimen without thecal spines (x7).



Figure 6. Synrhabdosome with two different genera. Paralectotype of *Orthograptus ruedemanni* (NYSM 4920). This synrhabdosome contains a specimen of *Lasiograptus* sp. (specimen with labeled arrows, lower right-hand corner, NYSM 16173). BS=bifid spine, PL=pleural list. Also note that several specimens have apertural spines and are probably *O. rivai* n. sp. Thus this synrhabdosome is composed of specimens from two different genera and three species (x7).

Utica Shale at Neuville, although they were not figured.

As previously noted by Rickards (1975) and Walters (1977), the central organs in the synrhabdosomes of *Orthograptus ruedemanni* figured by Ruedemann (e.g., 1908, Pl. 27, figs. 11 and 12) do not exist, nor were any found in synrhabdosomes collected in this study. Acceptance of synrhabdosomes as taphonomic associations also challenges Kirk's (1978) hypothesis that synrhabdosomes represent an adaptation to a benthic lifestyle in certain graptoloids.

Orthograptus ruedemanni can be distinguished from members of the *O. quadrimucronatus* group by its narrower, parallel-sided rhabdosome and by the absence of paired apertural spines and a median septum. It can be distinguished from members of the *O. amplexicaulis* group by the presence of a subapertural spine on $th1^2$ and by the amplexograptid form of the proximal end in the latter group. *Orthograptus ruedemanni* is differentiable from *O. rivai* n. sp., with which it commonly occurs, by the absence of paired apertural spines, a smaller angle of inclination of $th1^1$ to the rhabdosome, and the distinct-

VARIABLE	FUNCTION 1	FUNCTION 2	FUNCTION 3
HVS	0.1495	0.2678	0.9767
HGT $Th1^1$	0.8060	-0.5708	-0.5616
WD $Th1^2$ Ap	0.1006	0.3243	-0.2037
WD $Th2^1$ Ap	-0.3223	0.2382	0.1598
WD $Th3^1$ Ap	0.2834	-0.9353	0.4479
WD $Th3^2$ Ap	0.2492	0.3138	-0.2575
RW 1	0.4337	0.3997	0.1439
RW 2	-0.3173	0.6267	0.004

Table 2. Standardized canonical discriminant function coefficients. Variable abbreviations correspond to the measurements displayed and explained in Figure 3.

ly shorter length of the visible part of the sicula on the obverse side of the colony.

Collection horizons.—0.5, 2.5, and 5.0 m in the measured section, left bank of the Jacques Cartier River, 2.4 km south of Pont Rouge (Figure 2). Uppermost *Orthograptus ruedemanni* Zone.

ORTHOGRAPTUS RIVAI n. sp.
Plate 2A-H, Figure 4P-Q

Etymology.—Named after Dr. John Riva.

Material.—Thirty isolated three-dimensionally preserved specimens from the Grondines Member at the Jacques Cartier River locality, and several flattened specimens from outcrops in the lower part of the Utica Shale along Chuctanunda Creek near Minaville, New York State. Holotype is ROM 4583, paratypes ROM 4584-4606.

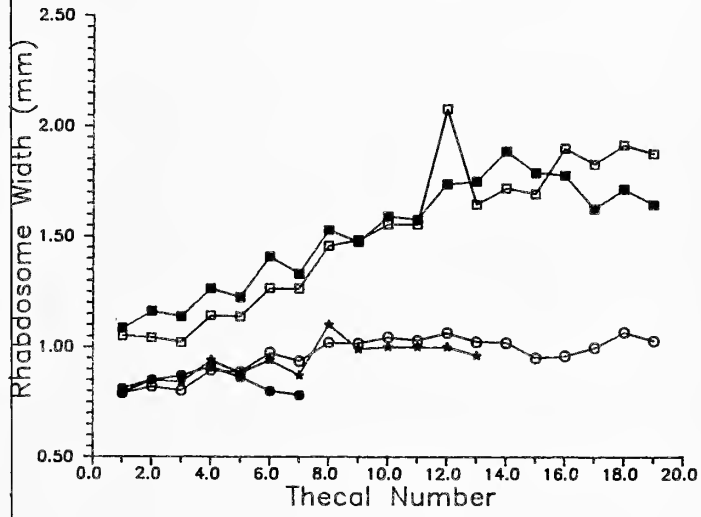


Figure 7. Rhabdosome widths of specimens of species of Orthograptus. Scatter plot showing rhabdosome widths (inter-aperture widths) of five groups of specimens. Closed squares are flattened specimens of *O. quadrimucronatus micracanthus* from the lower part of the Utica Shale at Locality 2, 0-15 m in a measured section; open squares are the same from 22-30 m. Open circles are flattened specimens of *O. ruedemanni* from Locality 1; closed circles are isolated specimens of *O. ruedemanni* from 2.5 m in the measured section at Locality 1. Stars represent isolated specimens of *O. rivai* n. sp. from 0.5 m in the measured section at Locality 1. Note that flattening does not distort measures of rhabdosome width when inter-aperture widths are used. Thecae are numbered consecutively on the X-axis where 1= $Th1^1$, 2= $Th1^2$, 3= $Th2^1$ etc.

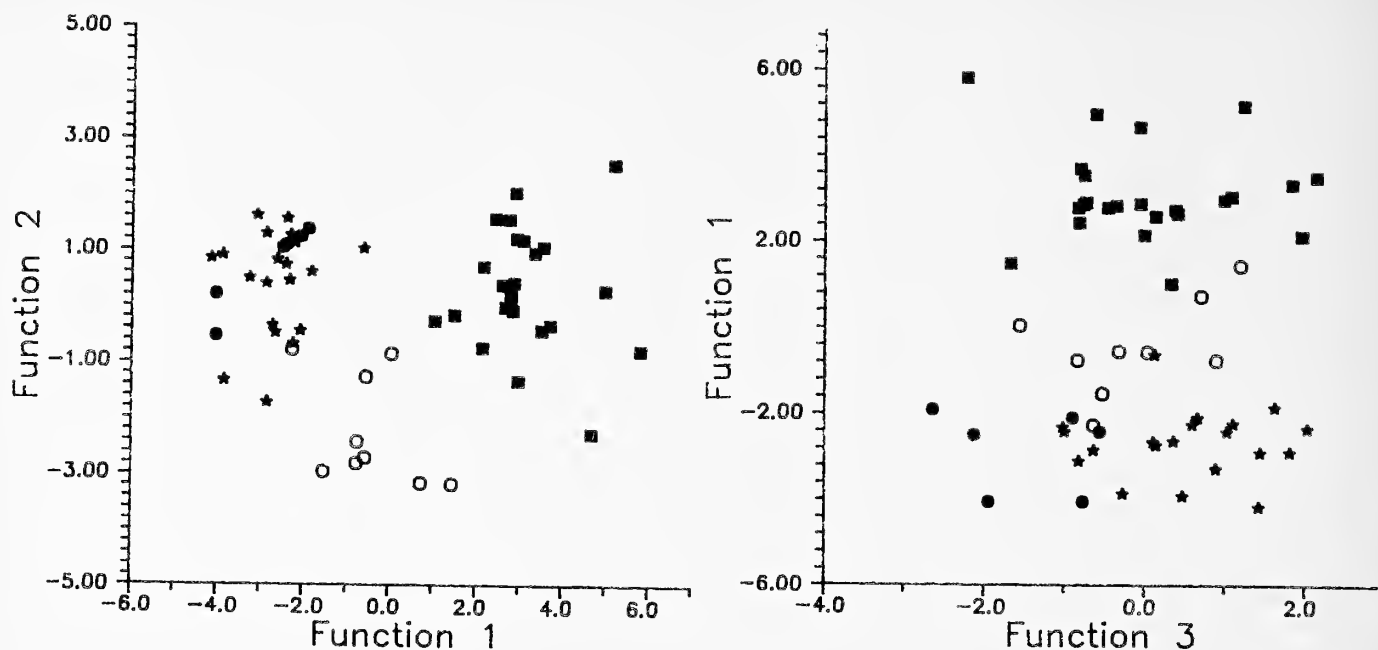


Figure 8. Discriminant analysis. Canonical discriminant function plots of specimens of species of *Orthograptus*. Closed squares represent specimens of *O. quadrimucronatus micracanthus*, open circles are flattened specimens of *O. ruedemanni*, closed circles are isolated specimens of *O. ruedemanni*, and stars are isolated specimens of *O. rivai* n. sp.

Diagnosis.—Species of *Orthograptus* with narrow rhabdosomes (maximum 1.3 mm), parallel sided; thecae orthograptid, $th1^1$ with apertural spine, $th1^2$ with sub-apertural spine, remaining thecae with short paired apertural spines.

Discussion.—As noted above, this species can be differentiated from *Orthograptus ruedemanni* by the presence of paired apertural spines on its thecae, a larger angle of inclination of $th1^1$ to the rhabdosome, and the distinctly longer portion of its sicula that remains visible in obverse view. It can be differentiated from *O. quadrimucronatus micracanthus* by its much narrower, aseptate rhabdosome.

Horizon.—0.5 and 5.0 m in the measured section on the Jacques Cartier River. Uppermost *Orthograptus ruedemanni* Zone.

Subfamily LASIOGRAPTINAE Lapworth, 1880, emend. Mitchell, 1987

Genus NEUROGRAPTUS Elles and Wood, 1908 (in 1901-1918)

Type species.—*Lasiograptus margaritatus* Lapworth, 1876 (subsequent designation by Bulman, 1929, p. 179).

Emended diagnosis.—Lasiograptines bearing thecae with extremely short supragenicular walls proximally, becoming orthograptid distally; each theca bears an apertural spine that bifurcates and connects to a well-developed lacinia. Thecae sclerotized, periderm attenuated; scopulate processes variably developed, clathria well-developed; proximal end structure corresponds to Pattern G primordial astogeny.

NEUROGRAPTUS MARGARITATUS (Lapworth, 1876)
Plate 2, figure I; Figure 4L-O

Lasiograptus margaritatus LAPWORTH, 1876, Pl. 2, fig. 60; LAPWORTH, 1877, p. 135, Pl. 4, fig. 25.

Lasiograptus (Neurograptus) margaritatus Lapworth. ELLES AND

WOOD, 1908, in 1901-1918, p. 332-333. Pl. 34, figs. 6a-e, Fig. 219a, b.

Lasiograptus (Thysanograptus) eucharis (Hall). RUEDEMANN, 1912, p. 84-85, figs. 24-28; RUEDEMANN, 1947, p. 461, Pl. 82, figs. 4, 8-11; (not Pl. 82, figs. 1-3, 5-7, 12-26).

Neurograptus cf. *N. margaritatus* (Lapworth). CLARK AND STRACHAN, 1955, p. 269, Fig. 4c.

Neurograptus margaritatus (Lapworth). RIVA, 1969, p. 521, Fig. 3d, e; WALTERS, 1977, p. 949, Pl. 2, fig. k; WILLIAMS, 1982, p. 252-253, Fig. 15a-f; FINNEY, 1986, p. 444, Fig. 9g, h.

Type specimen.—A specimen that matches Lapworth's (1876, Pl. 2, fig. 60) original figure has yet to be found (Strachan, 1971, p. 46).

Material.—One isolated three-dimensional specimen (a distal fragment) and six flattened specimens. The flattened material was collected from outcrops of the lower part of the Utica Shale (lower *Climacograptus spiniferus* Zone) at Neuville, Quebec.

Emended diagnosis.—*Neurograptus* species with aseptate rhabdosome; thecae orthograptid with apertural spines that bifurcate and connect to dual vertical threads that form a well-developed ventral lacinia. Thecae sclerotized; periderm in distal thecae consists of cortical tissue only, fusellar layer absent. Scopulate processes absent.

Description.—Inter-aperture widths increase from 0.6-0.7 mm at the first thecal pair to 0.75-0.9 mm at the eighth thecal pair, and after the tenth or eleventh thecal pair the rhabdosome tends to narrow. Thecae number eight to nine in the first 5 mm of the rhabdosome and decrease to seven to eight distally. Thecal overlap is small, only about 1/4 of the length of each theca. Thecae are orthograptid, with slightly everted apertures, each outlined by an apertural list. A sturdy spine arises at the intersection of the apertural and pleural lists and bifurcates laterally to connect with dual vertical threads and form a double ventral lacinia.

The periderm of distal thecae is thin, consisting of cortical tissue only. A fusellar layer is absent (Plate 2, figure I). The intersections of the ventral and lateral thecal walls are strengthened by a pair of pleural

lists that extend from the apertural list of the preceding theca to the base of a bifid spine, where they unite. Dorsal lists zigzag across the rhabdosome to form the dorsal margins of each theca. A short parietal list connects each dorsal list (at its point of intersection with the following dorsal list) with an apertural list (Plate 2, figure I; Figure 4N, O). Within the rhabdosome, an aboral list connects the reverse and obverse side parietal lists to form the base of each interthecal septum. The nema is connected to each aboral list by a short bar within the rhabdosome. This condition is reminiscent of other aseptate members of the Orthograptidae.

Discussion.—The isolation of a well-preserved fragment of *Neurograptus margaritatus* adds substantially to our knowledge of *Neurograptus*. It confirms the cortical nature of the periderm that is so poorly preserved in flattened material, and allows emendation of Elles and Wood's (1908, in 1901-1918) original diagnosis. In addition to other differences, specimens of *Neurograptus* can be distinguished from *Lasiograptus* by their lack of fusellar tissue in distal thecae.

Based on the information provided by the isolated specimen and material figured by Finney (1986, Fig. 9g,h), it is likely that the specimens described by Strachan (1974, p. 103-104, Pl. 2, figs. 4, 5, 8, Fig. 3) as *Neurograptus? bulmani* are more closely related to *Pipigraptus sooneri* Whittington (1955) than to *Neurograptus margaritatus*. True *Neurograptus* lacks the well-developed supragenicular walls and subapertural lists that characterize pipigraptid thecae (Mitchell, 1988). *Neurograptus* species also lack the complex, highly developed encircling lacinia found in *Pipigraptus bulmani* and *P. sooneri*. Thus in contrast to the suggestions of Mitchell (1987, p. 383), *Neurograptus* and *Pipigraptus* differ significantly in their thecal structure and are not synonymous.

The arrangement of clathria in *Neurograptus margaritatus* and their enclosure by cortical periderm are, however, strikingly similar to these features in *Orthoretiolites hami* Whittington. *Neurograptus*, *Orthoretiolites*, and other lasiograptids share a common clathrial architecture and the bifid genicular spine that arises at the union of the pleural lists. However, proximal thecae of *N. margaritatus* exhibit evidence for an extremely short supragenicular wall above the genicular spine. This suggests that the thecal architecture of *N. margaritatus* may represent a degenerate structure that retains a vestige of the lasiograptid thecal aperture. Additionally, the nema of *O. hami* forms a vertical bar to which the parietal lists are connected on the obverse side of the rhabdosome. The nema of *N. margaritatus*, in contrast, is entirely internal.

The similarity of the *Neurograptus margaritatus* and *Orthoretiolites hami* thecal architectures, in turn, supports Mitchell's (1987, p. 383) suggestion that *O. hami* is a yet more highly derived, structurally simplified lasiograptid. The supragenicular structure and lacinia are entirely lost and the genicular spine retained as an apertural spine in *Orthoretiolites*.

Horizon.—2.5 m in the measured section on the Jacques Cartier River (Figure 2). Uppermost *Orthograptus ruedemanni* Zone.

Family MONOGRAPTIDAE Lapworth, 1873, emend. Mitchell, 1987
Genus NORMALOGRAPTUS Legrand, 1987

Type species.—*Climacograptus normalis* Lapworth, 1877.

NORMALOGRAPTUS MOHAWKENSIS (Ruedemann, 1912)
Plate 1, figures J-N; Plate 3, figures A-B; Figure 4R

Diplograptus (Mesograptus) mohawkensis RUEDEMANN, 1912, pp.

80- 82, Pl. 2, figs. 18, 19, Figs. 19, 20; RUEDEMANN, 1947, pp. 419- 420, Pl. 71, figs. 24-28.

Climacograptus mohawkensis (Ruedemann). WALTERS, 1977, pp. 937- 938, Pl. 2, figs. f, h, i.

not *Climacograptus mohawkensis* (Ruedemann). WILLIAMS, 1982, p. 246-247, Fig. 10e-j.

Type specimen.—NYSM 10365, figured by Ruedemann (1912, Pl. 2, fig. 18; Fig. 19), from Swartztown Creek, New York State.

Material.—Fifteen isolated three-dimensionally preserved specimens from the Grondines Member on the Jacques Cartier River and hundreds of flattened specimens from the lower part of the Utica Shale at Neuville, Quebec.

Emended diagnosis.—A *Normalograptus* species with small rhabdosome, narrow; widens gradually to 1.0 mm (inter-aperture width); thecae climacograptid; proximal end with virgella only, conforms to a Pattern H primordial astogeny.

Description.—The rhabdosome is short, generally less than 15 mm in length. Thecae are climacograptid, numbering 7.5-8.0 in the first 5 mm, decreasing to seven in 5 mm distally. Narrow rhabdosomes widen gradually; inter-aperture widths increase from 0.4-0.5 mm at the first thecal pair to a maximum width of 0.75-0.85 mm at the ninth thecal pair.

Thecae are geniculate but lack genicular flanges. Supragenicular walls straight to gently convex, inclined slightly to the rhabdosome, and approximately 0.4 mm high at th2¹, increasing to 0.5-0.55 mm distally. Th1¹ and th1² are relatively long compared to the next few thecae. Thecal apertures are everted proximally, become horizontal distally, and lack well-developed selvages. The rhabdosome generally becomes septate at the base of the sixth thecal pair, although considerable variation is observed in the level of septal insertion (aseptate, see Plate 3, figure A; and insertion at the 11th thecal pair, see Plate 3, figure B).

The proximal end structure corresponds to a Pattern H primordial astogeny (Mitchell, 1987). The sicula is relatively short (approximately 1.0 mm) and broad and bears only a short virgella. The proximal end is narrow and fusiform with the virgella slightly incurved across the sicula aperture. The metatheca of th1¹ is tightly upturned and has a complete dorsal wall. This differentiates *Normalograptus mohawkensis* from *N. brevis*, whose th1¹ metatheca lacks a dorsal wall and is connected to the sicula only by a short bar (Bulman, 1944-1947). The structure of th1¹ in *N. mohawkensis* is, however, similar to that of another Pattern H species, *Glyptograptus kuckersianus* Wiman (see Mitchell, 1987).

Discussion.—*Normalograptus mohawkensis* is a key index species to the *Orthograptus ruedemanni* Zone. Riva (1974) has suggested that *N. mohawkensis* evolved from *N. brevis strictus*, a species common in the older *Corynoides americanus* Zone. However, the type specimen of *N. mohawkensis* (NYSM 10365, Figure 4R herein) was collected from rocks that, based on regional geologic studies (Ruedemann, 1912), are from the lower *Corynoides americanus* Zone. Furthermore, Ruedemann's (1919) oldest graptolite zone for the Utica Shale of the Mohawk Valley in New York State was the *Mesograptus mohawkensis* Zone (=lower *Corynoides americanus* Zone of Riva, 1974). Thus either *N. mohawkensis* has a much longer range than previously recorded, or the name "*N. brevis strictus*" is a junior synonym for "*N. mohawkensis*." This means that the younger (*Orthograptus ruedemanni* Zone) normalograptids will need a new name.

Specimens of "*Climacograptus*" *minus* figured by Elles and Wood (1906, in 1901-1918, Pl. 27, figs. 1a-g, figs. 124a-d) and Williams (1982, fig. 10e-j) do not appear to be conspecific with specimens of *N. mohawkensis* examined herein. "*Climacograptus*" *minus*

is parallel-sided, has well-developed apertural selvages, and has narrow introverted proximal apertures. *Normalograptus mohawkensis*, as noted above, widens until the ninth or tenth thecal pair, lacks apertural selvages, and has everted proximal apertures. Additionally, the occurrence of "*C.*" *minimus* in Great Britain (upper *D. clingani* and *P. linearis* Zones) is far younger than that of *N. mohawkensis* in North America. A detailed morphometric analysis of *N. mohawkensis* and other Middle Ordovician *Normalograptus* and potentially related species (e.g., "*C.*" *minimus*, "*C.*" *mississippiensis*, *N. brevis*, *N. brevis strictus*, and "*C.*" *putillus*) is being undertaken in order to elucidate the evolutionary relationships within this group.

Family DIPLOGRAPTIDAE Lapworth, 1873, emend Mitchell, 1987

Subfamily CLIMACOGRAPTINAE Frech, 1897, emend Mitchell, 1987

Genus PSEUDOCLIMACOGRAPTUS Přibyl, 1947

Type species.—*Climacograptus scharenbergi* Lapworth, 1876.

Subgenus PSEUDOCLIMACOGRAPTUS (PSEUDOCLIMACOGRAPTUS) Přibyl, 1947
emend. Mitchell, 1987

PSEUDOCLIMACOGRAPTUS (PSEUDOCLIMACOGRAPTUS) SP.
Plate 2, figure J

Discussion.—Two fragmentary proximal ends were isolated in collections from the Grondines Member. On the better-preserved specimen (Plate 2, Figure J), $th1^1$ is torn away, as is the base of $th1^2$. However, the sicula is well-preserved, as are $th2^1$ and $th2^2$. The sicula is 0.85 mm long and bears a short nema. The thecal apertures are deep and slightly introverted. The primordial astogeny appears to be Pattern D (Mitchell, 1987). No specific identification can be made based on such fragmentary material. It is worth noting, however, that this is the first recorded occurrence of a pseudoclimacograptid in eastern North America between the *Corynoides americanus* and *Amplexograptus manitoulinensis* Zones (Riva, 1974).

Acknowledgments

This study was funded, in part, by Geological Society of America research grants 3988-88 and 4203-89. S.C. Finney and an anonymous reviewer reviewed the manuscript.

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Upper Devonian turbidites in western New York: Preliminary observations and implications

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Abstract

This report examines two characteristic elements of Upper Devonian turbidite deposition in western New York. One of these elements is a submarine fan lobe-fringe deposit that characterizes the South Wales Member of the Perrysburg Formation. Thin-bedded siltstones interbedded with shale typify this deposit; the siltstones exhibit sedimentary features, including massive bedding, that become exceptionally rippled to the west; other sedimentary structures include grooves, parting lineations, and flutes. These directional indicators display a partial radial flow pattern across westernmost New York that is consistent with a lobe-fringe interpretation and is not easily reconciled with a sheet-flow interpretation.

The second submarine fan element is a series of possible sand-lobe deposits that characterize the Nunda Member of the West Falls Formation. Sandstone/siltstone packets that consist of massive, thick sandstone beds interbedded with shale units typify the sand-lobe deposits; the sandstone beds have abrupt, lobate terminations. The thick sandstone beds of the Nunda Member do not appear to grade into the thin-bedded lobe-fringe sandstones. This observation suggests that lobe and lobe-fringe sandstones were deposited by two different types of turbidity flows: sand-rich, poorly efficient turbidity flows resulted in the sand-lobe deposits, whereas sand-poor, highly efficient turbidity flows resulted in lobe-fringe deposits.

Introduction

This preliminary report presents data gathered from ongoing research of sandstone/siltstone turbidites in two coarsening-upward clastic depositional cycles within the West Falls and Perrysburg Formations (Figure 1; in this report, these sandstone/siltstone turbidites will be referred to simply as "sandstones"). The many gorges and ravines in the area west of the Genesee Gorge ("western New York" in this paper; see Figure 2) provide the control necessary to trace individual sandstone beds across the region and to characterize the interrelationships of the sandstone beds and the lateral variability in bedforms, texture, and thickness. From these and other data, the western New York turbidites in this part of the Upper Devonian appear to represent lobe and lobe-fringe deposits on a submarine fan.

Stratigraphy and sedimentology of the Upper Devonian in western New York

Overview

The Upper Devonian in western and central New York records an infilling of the Catskill Sea from sources to the east. The Upper Devonian in this region consists of a number of major sedimentation cycles; each coarsening-upward cycle is marked by a basal black shale that grades upward into grey and greenish-grey shales which, in turn, are interbedded with sandstones near the top of each cycle (e.g., Pepper and de Witt, 1951; Pepper et al., 1956; Sutton, 1963; Buehler and Tesmer, 1963; Kirchgasser and House, 1981; van Tyne, 1982, 1983; Sevon and Woodrow, 1985). In addition, some cycles contain sandstones that lie directly on the black shale. Sandstones from both positions in the stratigraphic cycles are discussed in this report.

The origin proposed for these sandstones varies markedly among different units, different regions of the same unit, and different researchers. Paleocological studies have been conducted on a large number of Frasnian "sandy" sections in central New York (e.g., Bowen et al., 1970; Sutton et al., 1970; Thayer, 1974; McGhee and Sutton, 1981, 1983, 1985; Sutton and McGhee, 1985). These paleocological studies suggest that the Frasnian "Chemung" facies (sensu Caster, 1934) of central New York represents a collage of shallow marine environments that include delta front, delta platform, and channel/estuary environments. However, Craft and Bridge (1987) asserted that recent advances in sedimentology invalidate some of the assumptions implicit in the models of depositional environments proposed by paleocologically oriented researchers (e.g., Sutton et al., 1970; Sutton and Ramsayer, 1975; McGhee and Sutton, 1981). Thus Craft and Bridge (1987) believed that the depositional environments ascribed to particular Devonian sandstones by the paleocological researchers are open to reinterpretation. In western New York, preliminary paleocological studies of Devonian sandstones have been performed only very recently (Hasiotis and Piechocki, 1990).

Sedimentological studies typically have concentrated on a few isolated vertical sections in the lower sandy units of the Frasnian in central New York (Walker and Sutton, 1967; Woodrow and Isley, 1983; Craft and Bridge, 1987). These detailed studies suggest that sandstones in the western part of central New York represent turbidites deposited on the basin slope and floor (broadly, the "Portage" facies of Caster, 1934),

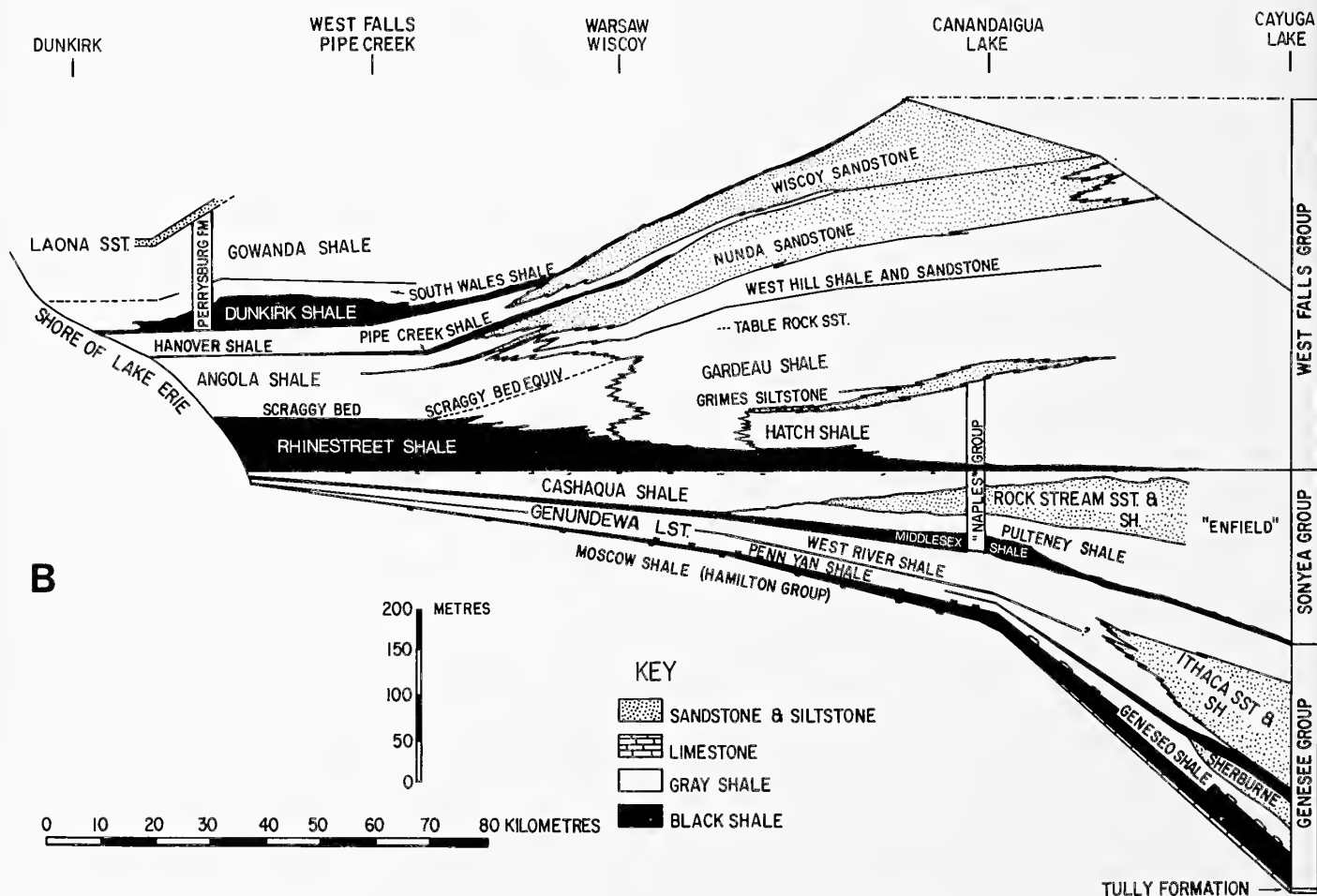
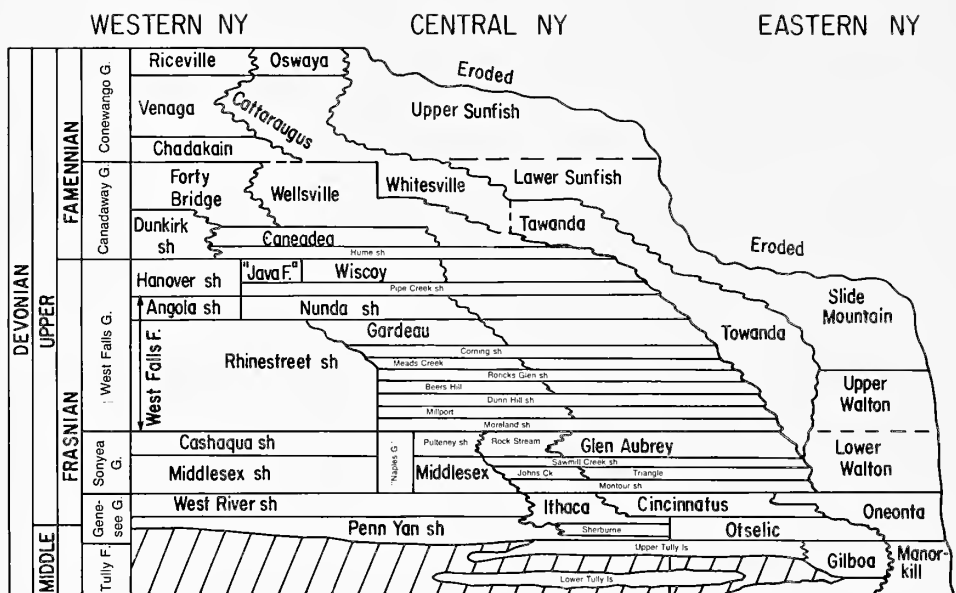


Figure 1. Stratigraphic correlation diagrams. A, Stratigraphic correlation diagram for the Upper Devonian of New York State (after Sevon and Woodrow, 1985, and Rickard, 1975). Following Sevon and Woodrow (1985), lithologies are not capitalized. In this chart, rocks of the Perryssburg Formation are included in the Dunkirk Shale. B, Facies diagram of the Upper Devonian in western and central New York (from Kirchgasser and House, 1981, and Johnson et al., 1985).

whereas some of the eastern sandstones represent platform storm deposits. Similar conclusions have been reached in sedimentological and paleoecological studies of "Portage" and "Chemung" facies south of New York State in the eastern and central portions of the Appalachian Basin (e.g., Lundegard et al., 1985; Van Tassell, 1987). However, in western New York, no sedimentological studies have been done of the sandy units in the Upper Devonian Portage facies since the early recognition of turbidites and storm deposits.

Devonian turbidites in the Catskill Sea generally have been thought to be more similar to nonchannelized ramp deposits than to modern submarine fan deposits (Woodrow and Isley, 1983; Woodrow, 1985;

Lundegard et al., 1985; Van Tassell, 1987). This clastic ramp model has invoked sheet flows from line sources due to storms rather than from point sources at channel mouths or narrow slide complexes. The arguments that support a clastic ramp model have centered on two lines of negative evidence: (1) absence of observed submarine channels (e.g., Walker and Sutton, 1967), and (2) lack of observed radial flow patterns in nonchannelized turbidites (Sutton, 1959; Colton, 1967; Walker and Sutton, 1967; McIver, 1970; Sutton et al., 1970; Thayer, 1974; Potter et al., 1979; Broadhead et al., 1982; Lundegard et al., 1985; Woodrow, 1985; Van Tassell, 1987).

However, our initial research in western New York has revealed a

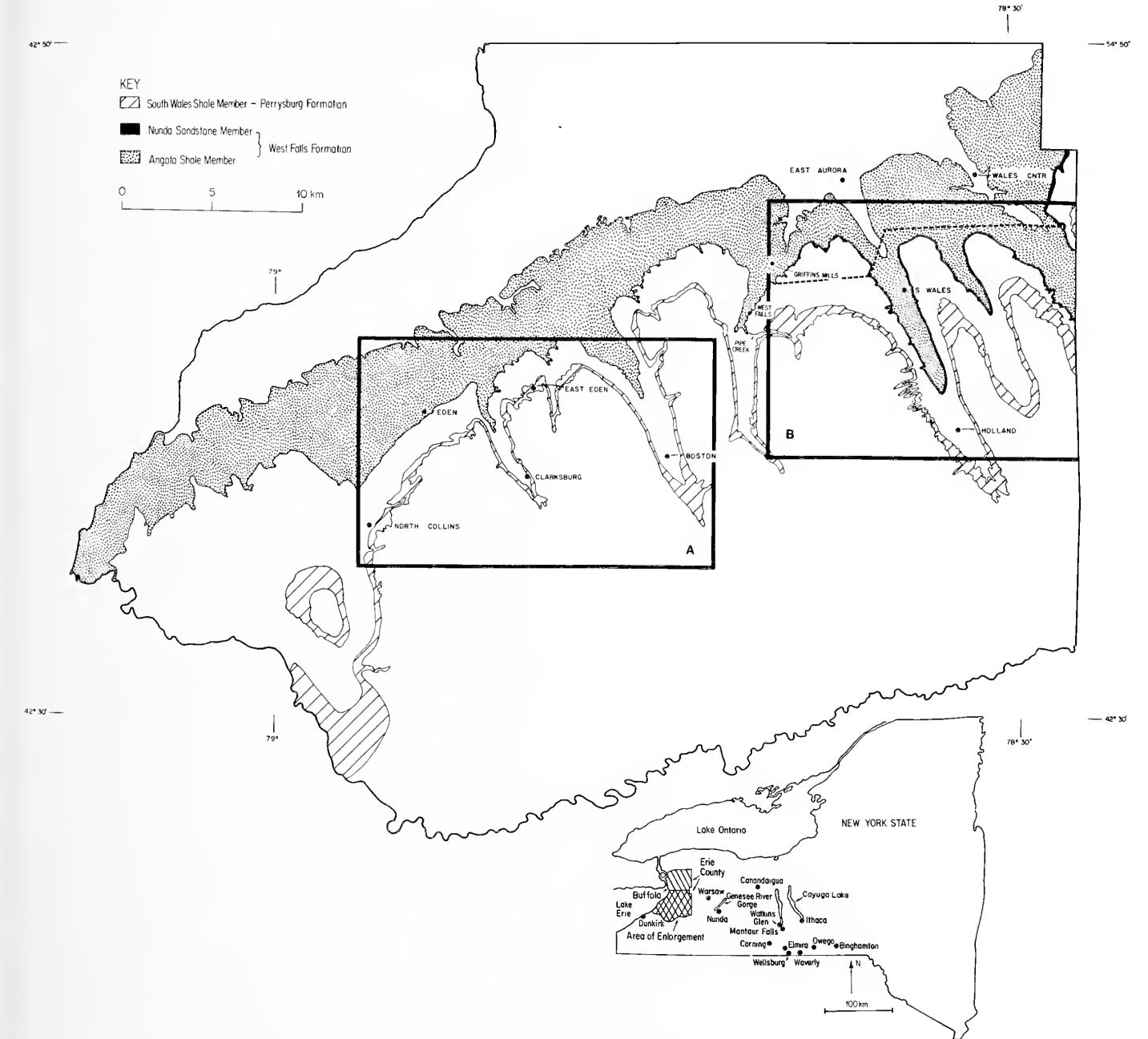


Figure 2. Distribution of Upper Devonian units discussed in text. Geologic map (after Buehler and Tesmer, 1963) is of Erie County; index map of New York State shows the location of the geologic map. Box "A" in Erie County shows location of South Wales Member maps (see Figures 3-8), and box "B" shows location of Nunda Member maps (see Figures 9-11). Dashed line in box "B" locates stratigraphic cross-section of Figure 9.

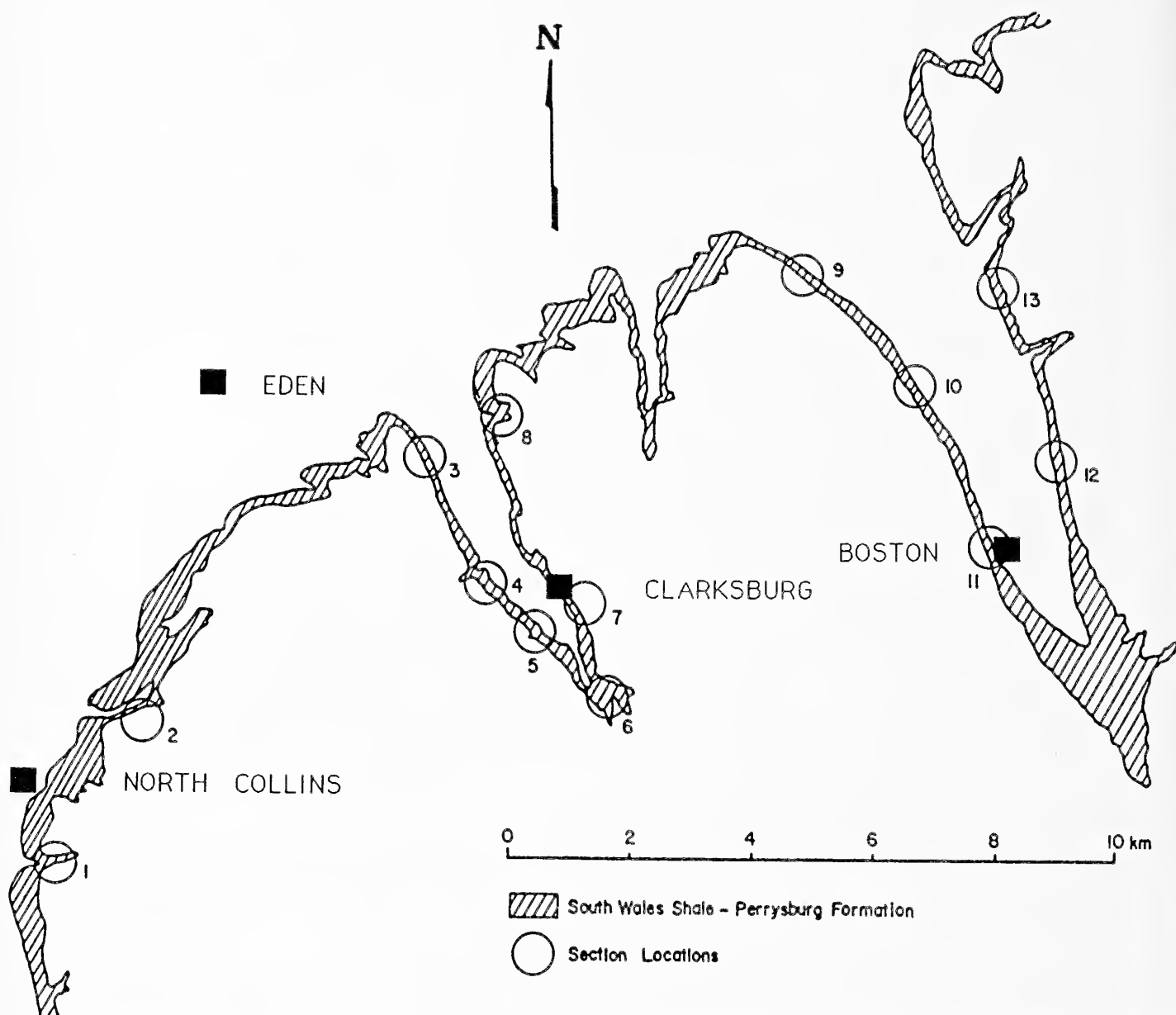


Figure 3. Map displaying locations of measured sections of the South Wales Member. For location of map, see Figure 2. Figure from Gutmann and Jacobi (1988) and Gutmann (1989).

systematic areal variation in paleoflow that describes a partial radial flow pattern of 40° over a distance of 18 km, and van Tyne (1982) identified possible macroscale submarine channels in the Upper Devonian sequence based on isopach variations. Thus a submarine fan model may be appropriate for the Upper Devonian turbidites in western New York.

Some investigators have also questioned whether it is appropriate to compare Devonian turbidity currents to modern turbidity currents because of possible low paleoslopes in the Catskill Sea (e.g., Lundegard et al., 1985). However, gradients on modern middle and outer submarine fans are extremely low, such as 0.03° to 0.09° on the Bengal Fan

(Emmel and Curray, 1985). These gradients are quite similar to the lowest gradients proposed for the Catskill Sea (ca. 0.02° ; see Woodrow and Isley, 1983).

Generalized description of "sandstone" units discussed in this report

Stratigraphic designations for the units discussed below have not been consistently employed (Clarke, 1903; Clarke and Luther, 1908; Hartnagel, 1912; Pepper and de Witt, 1951; Pepper et al., 1956; Buehler and Tesmer, 1963; Rickard, 1975; Kirchgasser and House, 1981; Sevon and Woodrow, 1985; compare Figure 1A and Figure 1B). The stratigraphic designations of Pepper and de Witt (1951), Pepper et al. (1956),

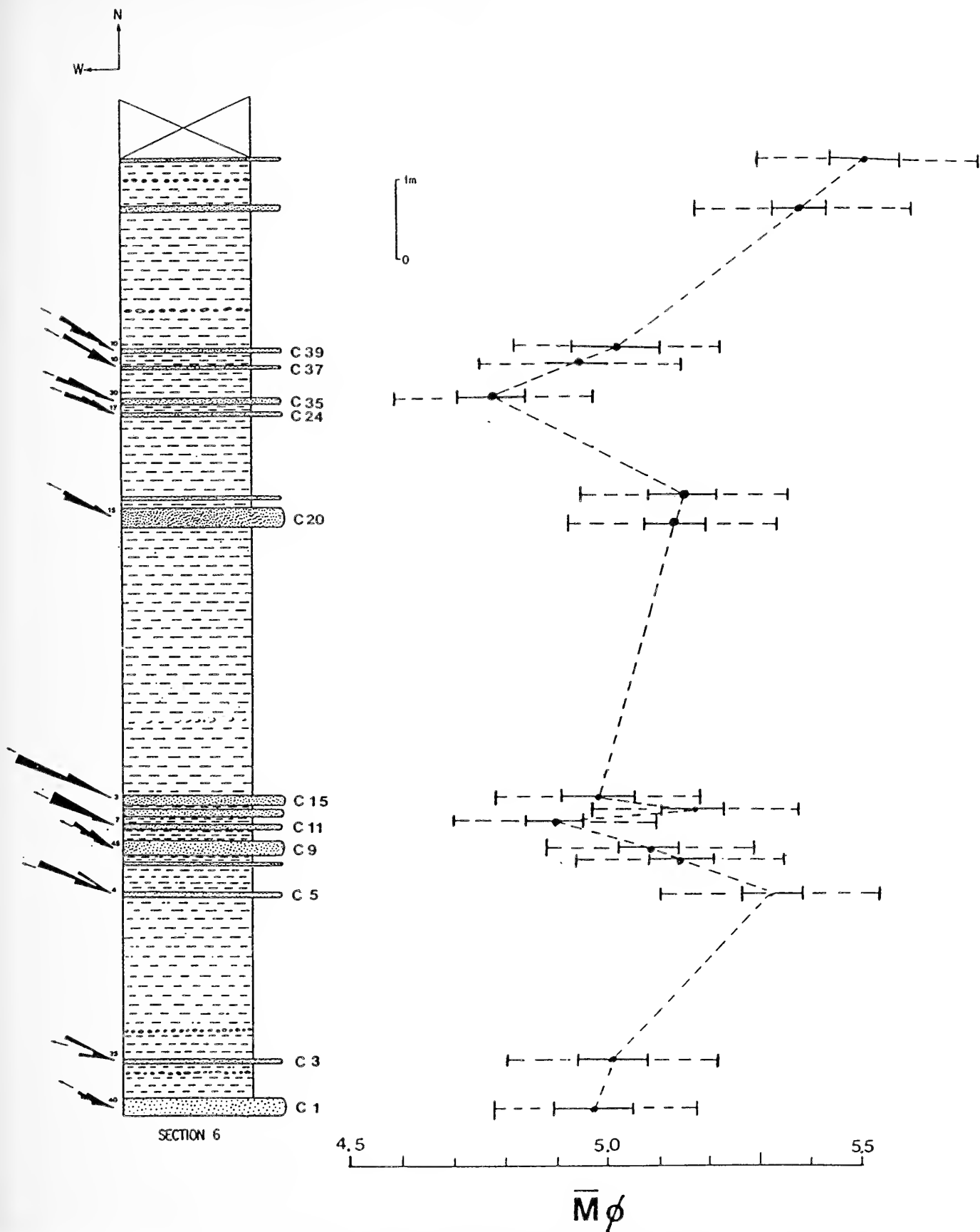


Figure 4. Columnar section of the South Wales Member at locality 6 and up-section grain size variations. Locality of measured section number 6 shown in Figure 3. In the columnar section, calcareous concretion horizons are indicated by small circles. Rose diagrams and averages for current indicators in sandstone units are shown left of the columnar section. Up-section variations in grain size are to the right of the columnar section. Solid error bar indicates sampling error and dashed error bar indicates measuring error. Figure after Gutmann and Jacobi (1988) and Gutmann (1989).

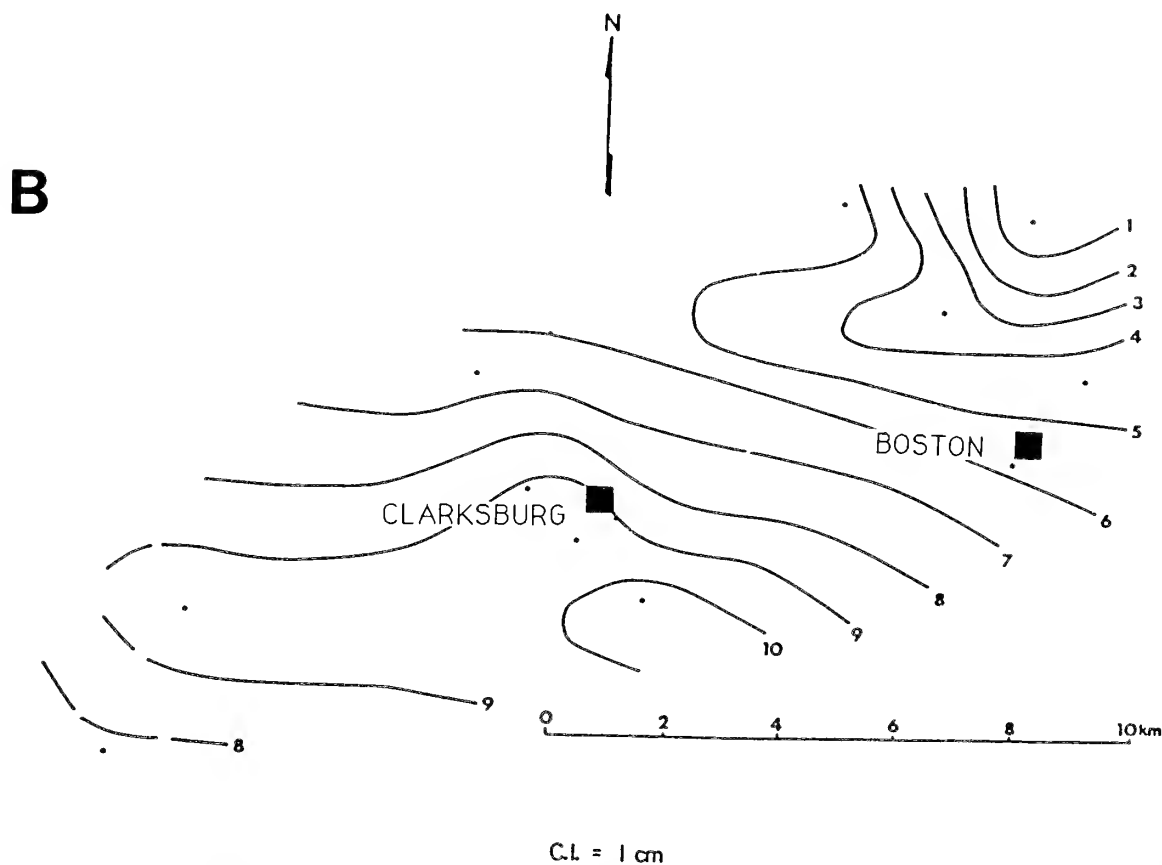
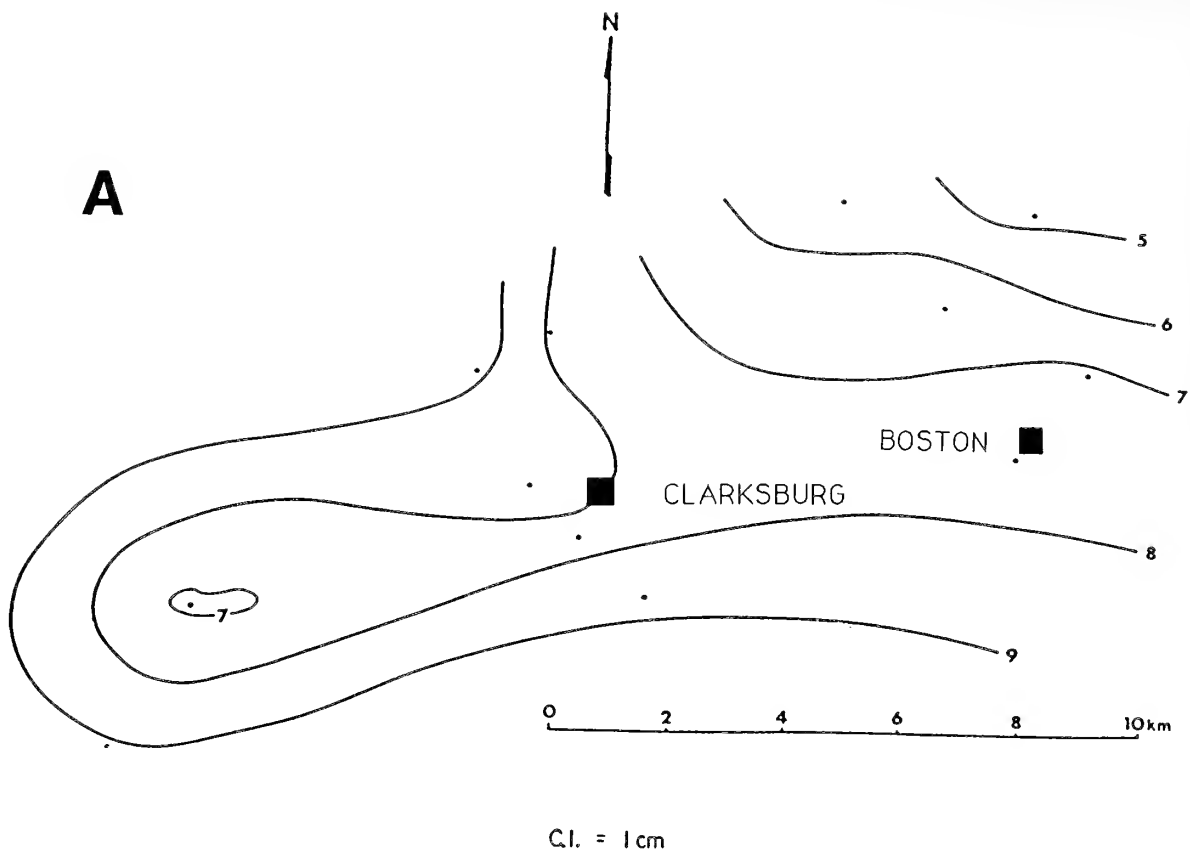


Figure 5. Sandstone thickness maps of the South Wales Member. A, Average sandstone thickness of the upper division of the South Wales Member. B, Average sandstone thickness of the lower division of the South Wales Member. In both figures, the measured sections are indicated by the dots. "C.I." is "contour interval." Figure from Gutmann and Jacobi (1988) and Gutmann (1989).

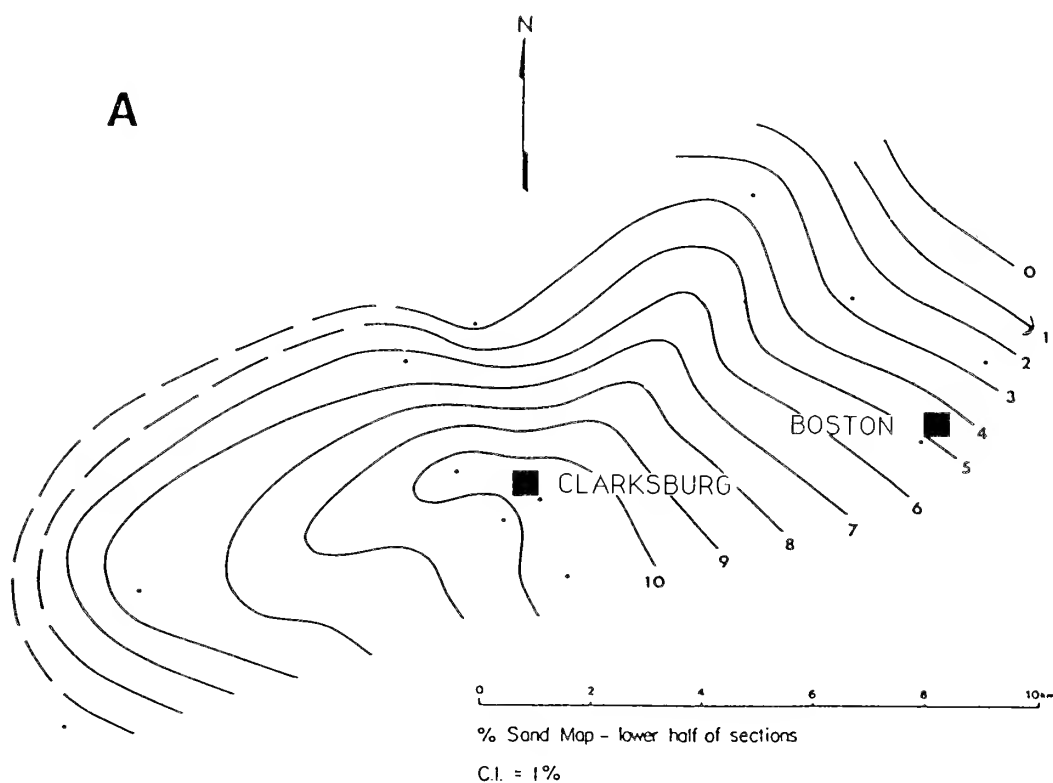
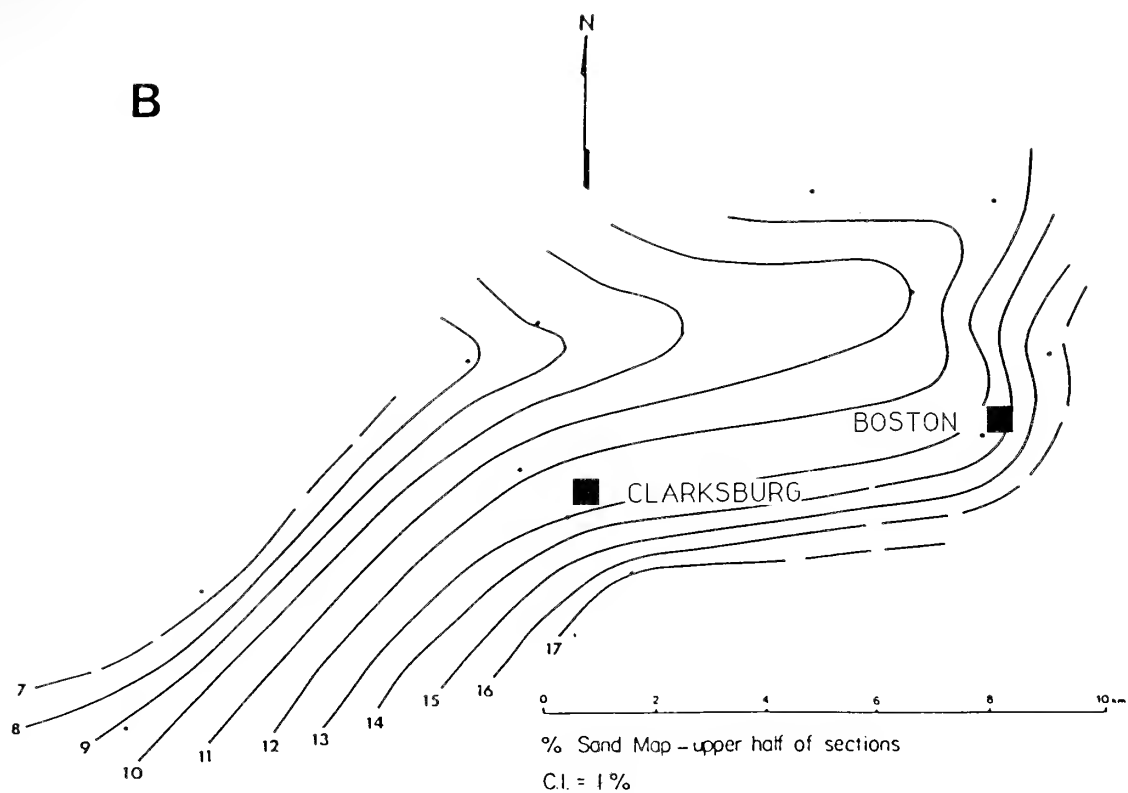


Figure 6. Sandstone percentage maps of the South Wales Member. A, Percentage of sandstone in the lower division. B, Percentage of sandstone in the upper division. "C.I." is "contour interval." Figure from Gutmann and Jacobi (1988) and Gutmann (1989).

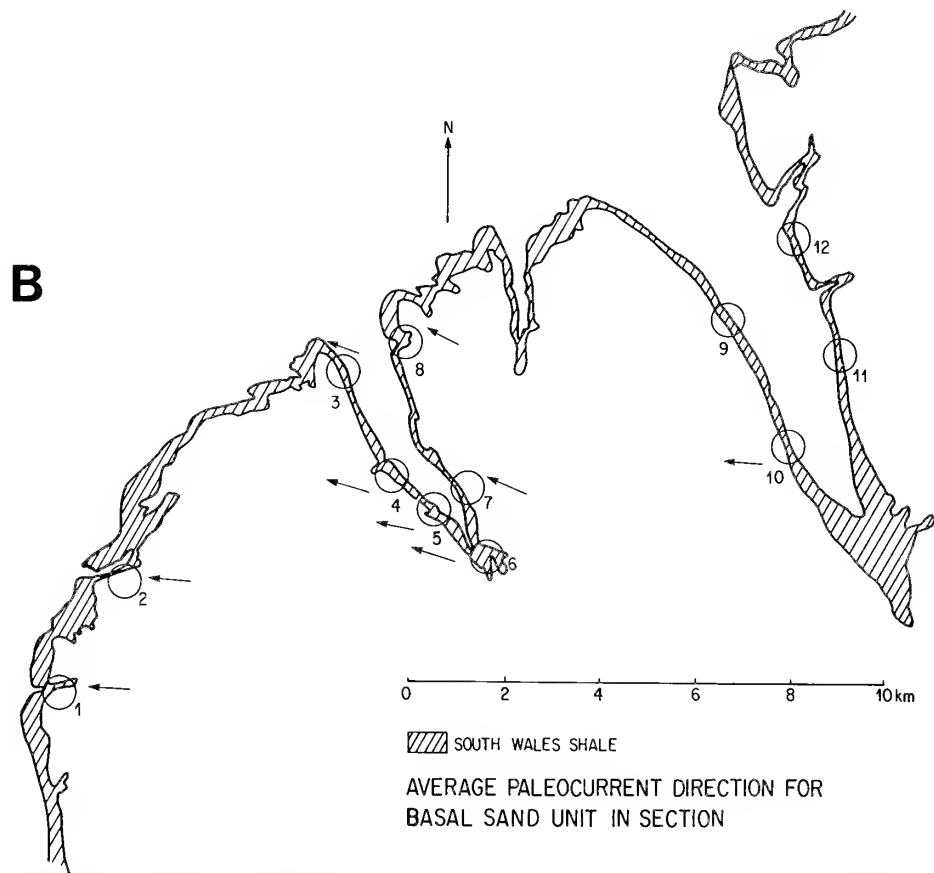
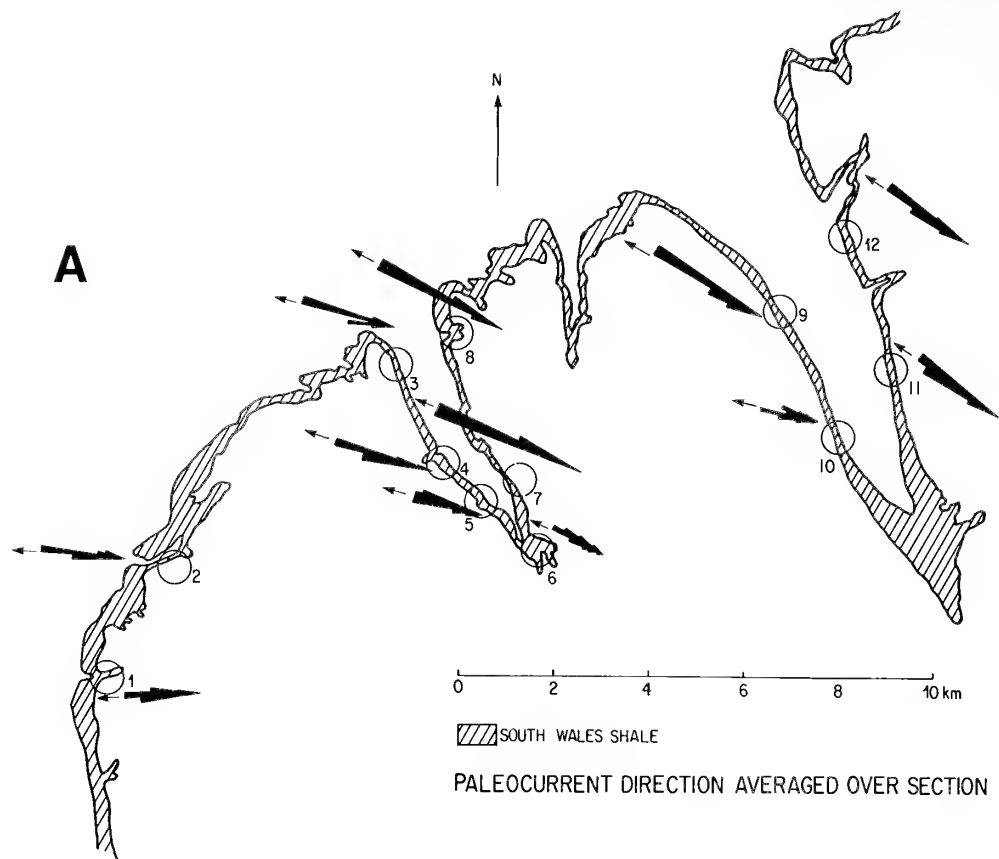


Figure 7. Paleocurrent directions maps of the South Wales Member. A, Paleocurrent directions for all sandstones at each measured section of the South Wales Member; arrow denotes average direction. B, Average paleocurrent direction for the basal sandstone unit in the South Wales Member. Figure from Gutmann and Jacobi (1988) and Gutmann (1989).

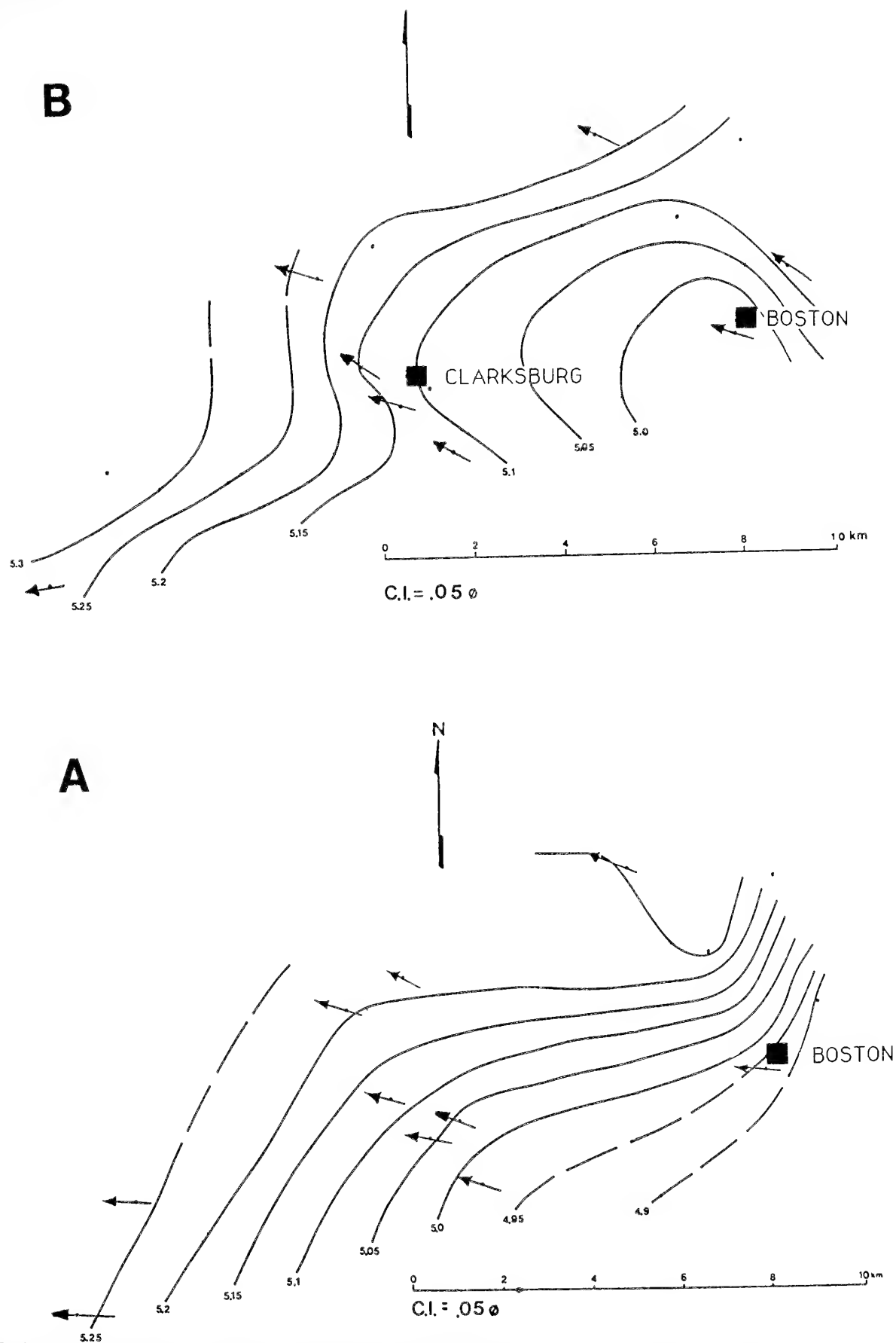


Figure 8. Grain size maps of the South Wales Member. A, Mean grain size of the basal sand unit of the South Wales Member. Arrows show flow directions of Figure 6B. B, Mean grain size of the basal sand of the upper division of the South Wales Member. Arrows represent flow directions inferred from current indicators observed in that sandstone bed. "C.I." is "contour interval." Figure from Gutmann and Jacobi (1988) and Gutmann (1989).

and Kirchgasser and House (1981) are employed in this report (Figure 1B) with the following exceptions: the lithic terms that were applied to the South Wales "Shale" Member and the Nunda "Sandstone" Member are dropped because, as discussed below, the lithologic terms are inappropriate for these heterolithic units in Erie County.

South Wales Member of the Perrysburg Formation (Pepper and de Witt, 1951).—The South Wales Member consists of fine-grained, thin-bedded sandstones and siltstones interbedded with greenish grey shale (Figure 1; Pepper and de Witt, 1951; Buehler and Tesmer, 1963). The South Wales Member thins from a maximum of 24 m at Lake Erie to a minimum of 6 m at the Genesee Gorge (Pepper and de Witt, 1951). The unit is distinguished from the overlying grey shales by the characteristic thin-bedded sandstones, and from the underlying black shale by both the sandstones and the grey shale. Because the only study of the South Wales Member that includes sedimentology predates most of the earliest publications on turbidites, the turbiditic nature of the South Wales Member sandstone units was not recognized; rather, Pepper and de Witt (1951) believed the sands represented stream deposits and delta deposits.

Nunda Member of the West Falls Formation (Clarke, 1897).—Near the Genesee Gorge, the Nunda Member consists of approximately 75 m of thickly bedded, amalgamated sandstones. The sandstone beds thin to the west and become interbedded with grey shale (Pepper et al., 1956; Buehler and Tesmer, 1963). Two sandstone packets extend westward to sharp pinchouts in central Erie County. Pepper et al. (1956) considered the shales that are interbedded with the sandstones as part of the Angola Shale. However, for ease of analysis and discussion, this report considers the shales between the sandstone tongues to be part of the Nunda Member. The sandstone beds commonly display either a massive or an undulatory, flaggy-bedded character (Clarke, 1897; Clarke and Luther, 1908; Pepper et al., 1956; Buehler and Tesmer, 1963). Two tongues of the Nunda Member extend westward to pinchouts in central Erie County (Pepper et al., 1956).

Preliminary results of ongoing fieldwork

South Wales Member.—In the western exposures (Figures 2 and 3), the South Wales Member can be divided into two units—a lower division with a relatively thick basal sandstone (bed C1 in section 6, Figure 4), and an upper division that also has a thick basal sandstone (bed C20 in section 6, Figure 4; see Gutmann and Jacobi, 1988; Gutmann, 1989). The lower division varies from 5.0 to 7.0 m thick, and the upper division ranges from 4.5 to 6.5 m thick. The lower division generally consists of two packets of sandstones—one at the base and one near the middle of the lower division (Figure 4). In several sections, the upper division also consists of two or more packets of sandstone beds (Figure 4). Within the lower division, the average sandstone bed thickness varies from about 5.0 cm in the northeast to more than 9 cm in the southwest and south-central areas (Figure 5B). The average sandstone thickness in the upper division varies from 1.0 cm to more than 10.0 cm (Figure 5A). The percentage of sandstone in the lower division varies from 0% to more than 10% (Figure 6). The isopach contours form a distinctly lobate pattern, which is somewhat consistent with the observed transport directions, especially in the western sections. The percentage of sandstone in the upper division varies from 7% to 17% (Figure 6).

The lower contacts of the thicker sands in the South Wales Member typically display abundant sole marks; these marks include groove casts, groove with chevron casts, bounce and prod marks, and some flute casts. Grooves and striations normal to the ripple crestlines are both prominent and abundant, and most likely were carved by water-

logged plant remains, although shell debris cannot be totally dismissed. Parting lineations are observed in both planar-bedded sandstones and rippled sandstones; the ripple crestlines are orthogonal to the parting lineations. Based on the sole marks and bedforms, paleocurrent determinations in all the sandstone units reveal an overall west-northwesterly transport direction (Figure 7). In detail, however, the paleoflow indicators on most individual beds display a systematic swing of about 40° over a distance of some 18 km across western Erie County (Figure 7).

In both divisions, the grain size generally increases to the southeast (Figure 8). The mean grain size of both basal sandstone beds is about 5 ϕ in the western sections, with a range from about 5.3 ϕ in the west to 4.9 ϕ in the east (Figure 8). The isopachs of the basal sandstone of the lower division are fairly regularly spaced and are generally transverse to the transport direction, whereas the basal sandstone of the upper division has a more distinctly lobate isopach pattern with contours relatively highly oblique to the transport direction on the margins of the lobe (Figure 8). Up-section variations in grain size are not especially distinctive in the few sections that have been analyzed. For example, the variability in grain size in section 6 is barely greater than the experimental error (Figure 4). Given these constraints, the most prominent patterns appear to be a coarsening-upward of the upper sandstone packet in the lower division, and a fining-upward of the upper packet in the upper division (Figure 4).

Many sandstone units display prominent straight-crested climbing ripples; these asymmetrical ripples are transverse to the current flow deduced from sole marks and parting lineations. Most of the sandstones exhibit Bouma sequences Tc and Tcd/e, and a few display Tbc, Ta, and Tab. In addition, the basal sandstone shows a systematic progression of Bouma sequences across Erie County: from Ta/Tab and Tbc in the east to Tc in the west. On the basis of the thickness and texture of the sandstones, Walker's (1967) ABC index, and the sand/shale ratio, most of the sandstones in the South Wales Member are "distal" turbidites. Significantly, the sandstone units generally lack such shallow marine or nearshore bedforms as hummocky cross-stratification and herringbone patterns, although a very limited number of beds in a few sections display small-scale bedforms similar to larger-scale hummocky cross-stratification.

A working hypothesis for the origin and depositional environment of sandstones in the South Wales Member can be constructed from the results of this preliminary study. First, as stated above, the bedforms are consistent with a "distal" turbidite origin. Second, individual turbidites appear to be nonchannelized because the sandstones do not show abrupt lateral changes in character (e.g., thickness) across Erie County, and because neither significant erosion at the basal contacts nor typical channel facies are observed.

The critical remaining question concerns the depositional setting of these nonchannelized "distal" turbidites. The thin-bedded and continuous nonchannelized nature of the sandstones, the sand/shale ratio, and the bedforms suggest that the thin-bedded sandstones are either (1) interchannel deposits (e.g., Mutti, 1977), (2) "distal" ramp deposits (e.g., Pickering, 1982; Chan and Dott, 1983), or (3) "sand lobe-fringe deposits" (see terminology of Mutti and Ricci Lucchi, 1975; Mutti, 1977; or "nonchannelized lobes" of Type I deposits in the terminology of Mutti and Normark, 1987).

Several considerations can be utilized to discriminate among the three possible depositional settings outlined above for the sandstone beds. Interchannel areas can be discounted as a suitable depositional setting because there are no known channel facies in the South Wales Member. Discrimination between ramp and fan deposits may be

TABLE 1

BOUMA SEQUENCE		SANDSTONE THICKNESS (in cm)		% SANDSTONE		
LF	BP	LF	BP	LF	BP	
T_{cde}, T_{bc}	T_{cde}	0.37-4.3	<4	12-78	<30	Mutti
T_{cde}, T_{bc}, T_{ab}		1-10		0-17		SWM

LF = lobe fringe

BP = basin plain

SWM = South Wales Member

Table 1. Comparison of lobe-fringe and basin plain sands to the South Wales Member. "Mutti" data from Mutti (1977).

achieved through evaluation of the regional flow patterns. Radial flow patterns are consistent with lobe-fringe deposits that develop downslope from a submarine channel mouth (e.g., Hampton and Colburn, 1967; Pickering, 1982) and are not typical of ramp (or modified ramp) deposits (e.g., Chan and Dott, 1983). In this field area, the 40° variation in paleoflow direction might represent a portion of the radial flow pattern. Thus a lobe-fringe depositional setting appears consistent with the field observations. However, the possibility that the radial flow pattern was caused by local variations in topography on a clastic ramp cannot be dismissed yet.

The bedding characteristics of sandstones in the South Wales Member are also very similar to lobe-fringe (LF) deposits defined by Mutti (1977), and, on the basis of Bouma sequence and sandstone thickness, are distinctly more "proximal" than his basin plain (BP) facies (Table 1).

Nunda Member.—In western New York, the Nunda Member generally includes two packets of sandstone beds—one at the base of the Nunda and one near (or at) the top of the Nunda Member (Figure 9).

The total number of sandstone beds in the Nunda Member varies from one to eight, and the total thickness of the Nunda Member varies from 0 m to 38 m (Figure 10). The sandstone/shale ratio of the Nunda Member is quite variable and has two trends: a north-south trend near the feather-edge of the sandstone beds in the west, and an east-west-trending low that lies east of the feather-edge (Figure 11). This low is primarily the result of an east-west zone of anomalously thin sands in the upper packet of the Nunda Member; this zone appears to lie, in part, above the thickest portion of the lower packet of sandstones. The mean grain size of the uppermost sandstone bed varies from 7.5ϕ in the central area to 8.2ϕ at the termination of the sandstone. The overall east-west trend of the grain size is coincident with the thickest zone of the Nunda Member. There are very few recognizable flow direction indicators in the Nunda Member; the few grooves that have been observed in the western sections are transverse or highly oblique to the local isopach contours for the upper and lower sandstone packets. Vertical escape burrows are common in the sandstones of the Nunda Member (e.g., Hasiotis and Piechocki, 1990), and indicate very rapid deposition.

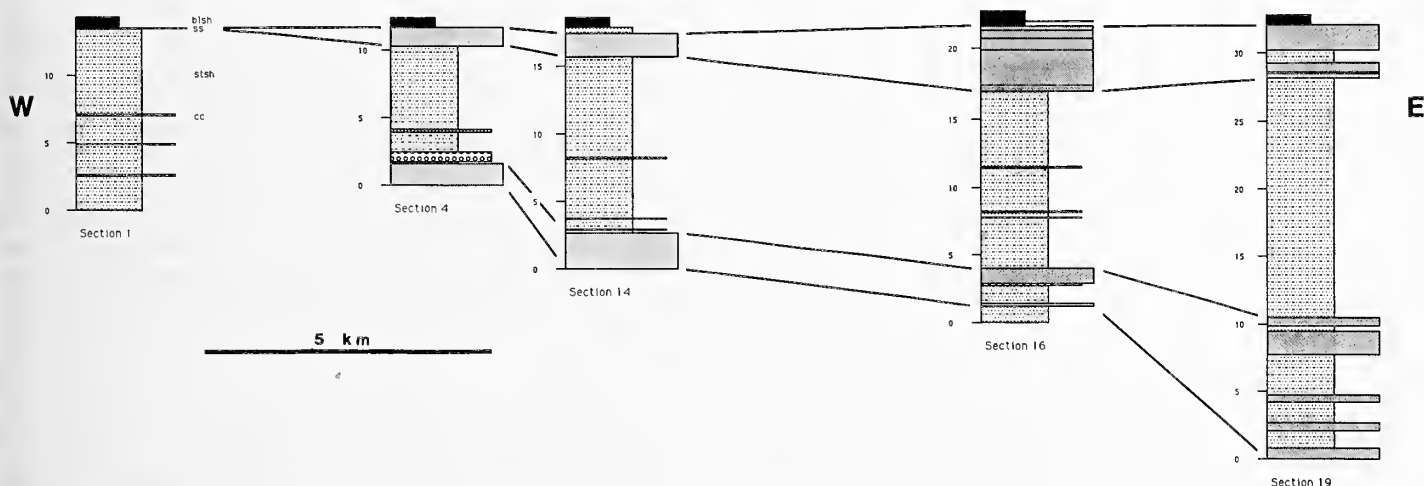


Figure 9. Simplified east-west stratigraphic cross-section of the Nunda Member. Location of cross-section shown in Figure 2; section locations shown in Figure 10. Vertical scale is in meters; "blsh" is "black shale," "cc" is "carbonate concretions," "ss" is "sandstone," and "stsh" is "silty shale and shaly siltstone." Figure after Piechocki et al. (1990) and Piechocki (1990).

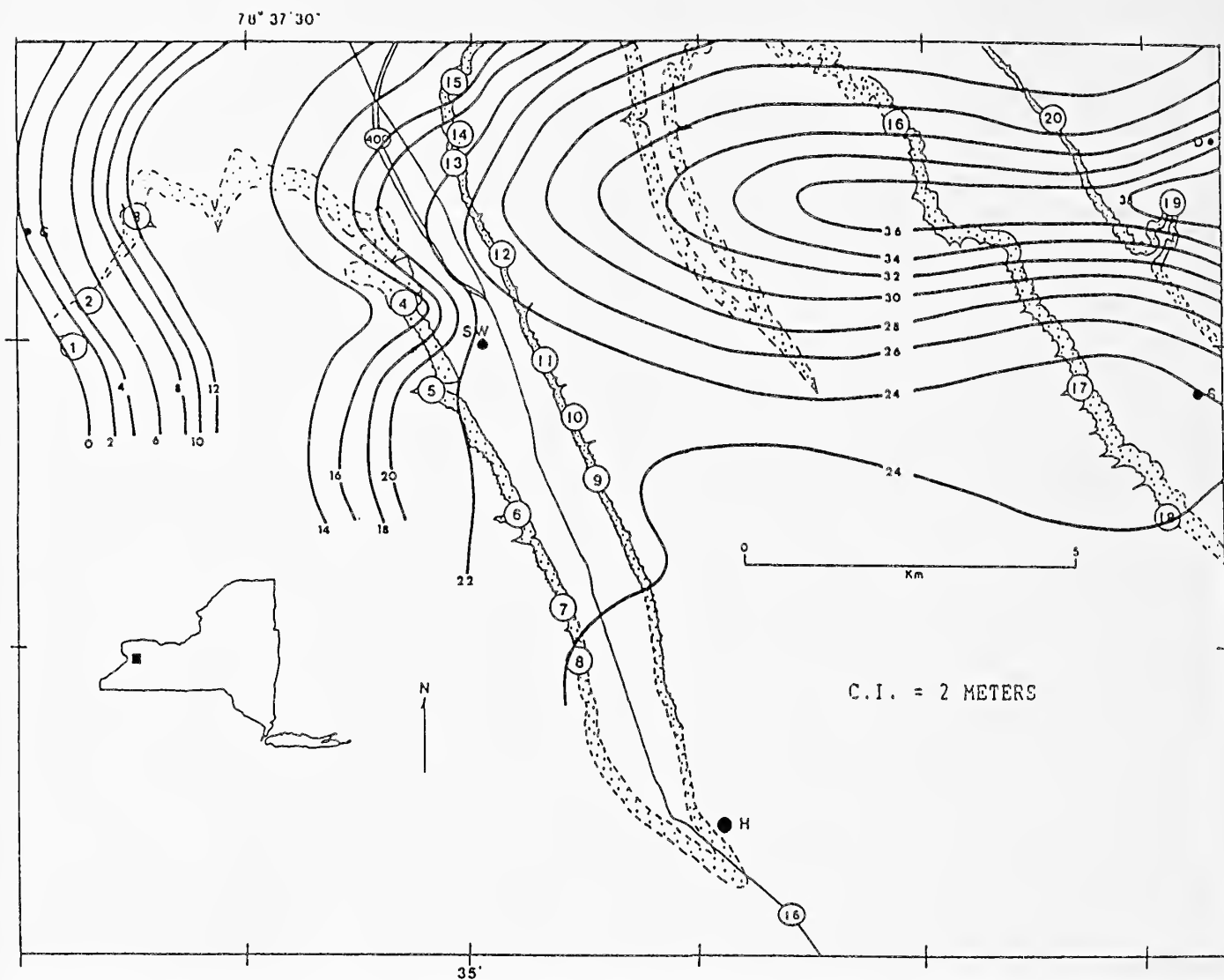


Figure 10. Isopach map of the Nunda Member. Location of map shown in Figure 2. Measured sections indicated by circled numbers. G=Griffin's Mills, H=Holland, S=Strykersville, SW=South Wales. "C.I." is "contour interval." Figure from Piechocki et al. (1990) and Piechocki (1990).

Reconnaissance work on the Nunda Member reveals that this unit is similar neither to "distal" turbidites (unlike sandstones in the South Wales Member) nor to "sheet sands" deposited from a line source. In addition, the Nunda Member sandstones are not similar to typical submarine channel sandstones; in outcrops throughout Erie County, the Nunda Member exhibits neither an erosive lower contact nor a channel facies. These observations, coupled with the massive character of the sandstone, its lobate nature (as indicated by flow directions, thickness, and grain size), and the thinning of the upper packet of sandstone over the thickest part of the lower packet (which suggests that the lower packet formed an area of positive relief at the time of deposition of the upper packet), are all consistent with the interpretation that the sandstones in the Nunda Member represent sand lobes on a submarine fan (Type II deposit of Mutti and Normark, 1987). However, other possible origins of the Nunda Member sandstones, such as deposits in a low-relief channel or relatively narrow mass flows of some sort, cannot be excluded from consideration at this point.

The abrupt termination of the "main" sandstone in the upper packet

near West Falls is an important characteristic of other sand-lobe terminations (e.g., Cazzola et al., 1985). Significantly, the pinchout near West Falls does not grade into the thin-bedded sandstones of the lobe-fringe deposits; this observation suggests that these lobe-fringe and sand-lobe deposits are caused by two different types of turbidity flows: sand-poor, highly efficient flow and sand-rich, poorly efficient flows, respectively. This terminology is similar to that developed for sand lobes (e.g., Mutti and Normark, 1987). Very preliminary research on sandstones of the Wiscoy Member (Figure 1) suggests that it is very similar to the Nunda Member, and that it too has a very abrupt termination.

Conclusions

The sandstone beds in the Upper Devonian South Wales Member and in the Nunda Member in western New York display characteristics that are believed to be analogous to deposits on submarine fans. The sandstone beds in the South Wales Member are fine-grained, thin-bed-

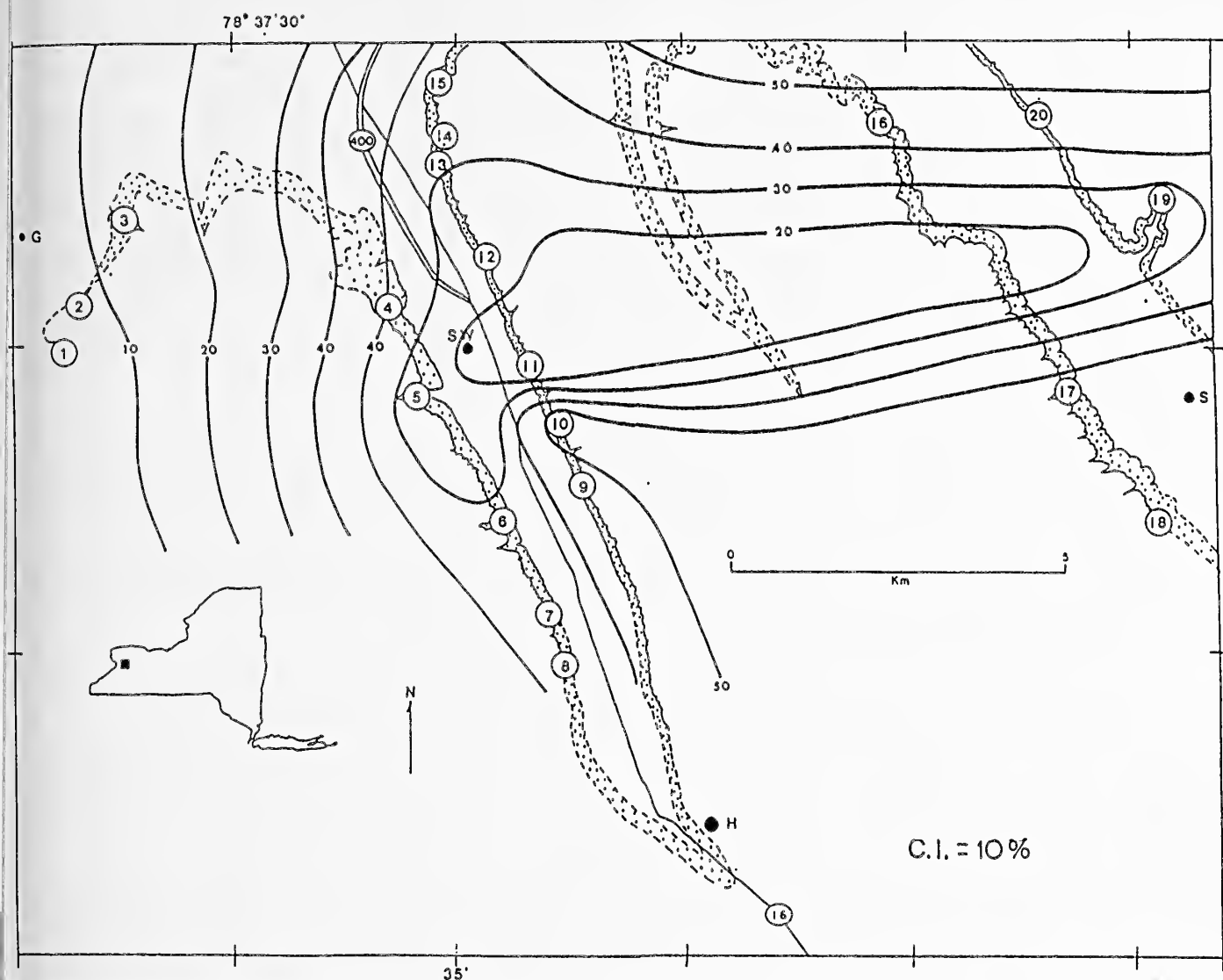


Figure 11. Sandstone/shale ratio map of the Nunda Member (in %). "C.I." is "contour interval." Figure from Piechocki et al. (1990) and Piechocki (1990).

ded, fairly continuous turbidites that appear to be similar to "lobe-fringe" deposits. Primary sedimentary structures, including groove casts, parting lineations, and sinuous-crested ripples, are internally consistent and indicate a partial radial flow pattern in western New York.

The sandstone beds in the Nunda Member are quite different from those in the South Wales Member. The Nunda Member sandstones are generally thick, massive to wavy/flaggy-bedded, and have few primary sedimentary structures. Isopach maps, grain size maps, and number-of-sandstone-bed maps all suggest that the Nunda sandstones have a lobate form near their terminations. These terminations are extremely abrupt; the sandstones do not "feather" out into the thin-bedded sandstones, as is typical of the South Wales Member sandstones. These characteristics suggest that the sandstones of the Nunda Member represent sand lobes on a submarine fan.

The lack of any gradation between the lobe and lobe-fringe facies suggests that the sand lobes were deposited by sand-rich, poorly efficient turbidity flows. By contrast, lobe-fringe sandstones were deposited by sand-poor, highly efficient turbidity flows.

Acknowledgments

We thank S. Hasiotis for enthusiastic help in field studies of the Nunda Member. This research was partly supported by NSF grant EAR 8904713 awarded to RDJ, SOC, and CM. G.C. Baird and D.L. Woodrow reviewed the manuscript.

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Early morphotypes of *Ancyrodella rotundiloba* at the Middle–Upper Devonian boundary, Genesee Formation, west-central New York

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Abstract

Early morphotypes of *Ancyrodella rotundiloba* (Bryant, 1921) are described from discontinuity horizons in the lower part of the grey Penn Yan Shale of the Genesee Formation between the Honeoye and Canandaigua Valleys in west-central New York. They mark the position of the base of the standard Lower *asymmetrica* conodont Zone and the Middle–Upper Devonian boundary, and they correlate with Montagne Noire Zone 1 in the zonation of Klapper (1989) and Klapper and Johnson (1990). The sections with the boundary-defining conodonts are some 100 km east (basinward) of the condensed western sections of the lower Genesee Formation where the position of the boundary is obscured by reworked faunas in the Leicester Pyrite and North Evans Limestone. The latter unit has the type horizon of *A. rotundiloba*. In the Honeoye Valley, the new collections are from lag deposits of detrital pyrite and phosphate debris at the top of a thin black shale that caps the Lodi Limestone (*norrisi* Zone of Klapper and Johnson, 1990; =Lowermost *asymmetrica* Zone) and from the base of a second black shale some 2.0 m above. Between the Honeoye Valley and Bristol and Canandaigua Valleys a few kilometers to the east, the Lodi Limestone is cut out, and the lower discontinuity horizon with *A. rotundiloba* descends to the base of the Penn Yan Shale at the contact with the underlying black Genesee Shale (?Upper *disparilis* Subzone of Klapper and Johnson, 1990). Missing at the boundary discontinuity in New York are the faunas of the uppermost Middle Devonian (Givetian) with *Ancyrodella binodosa* and forms transitional between *A. binodosa* and early morphotypes of *A. rotundiloba*. The alignment of the boundary in the ammonoid sequence in New York is in the lower part of the range of *Ponticeras*, below the entry of *Koenenites* and *Probeloceras*.

Introduction

In 1982, the Subcommittee on Devonian Stratigraphy (SDS) of the International Union of Geological Sciences (IUGS) recommended that the boundary between the Middle and Upper Series of the Devonian System and corresponding Givetian–Frasnian Stage be defined at the base of the Lower *asymmetrica* conodont Zone (Ziegler and Klapper, 1982b). The base of the Lower *asymmetrica* Zone is defined at the lowest occurrence of *Ancyrodella rotundiloba* (Bryant, 1921), an early species in the phylogeny of *Ancyrodella* and one long recognized in Devonian sections around the world (Ziegler and Werner, 1986). In

1987, the IUGS ratified the SDS recommendation to locate the Global Stratotype Section and Point (GSSP) at the base of Bed 42a' in the section at Col du Puech de la Suque (CPS-E) in the Montagne Noire, southwestern France. The critical lowest occurrence of *A. rotundiloba* in Bed 42a' is a morphotype named the "early form" by Klapper (1985, 1988). It is followed by a second morphotype (the "late form") that appears 0.5 m higher in Bed 46. A key consideration for selecting the base of the Lower *asymmetrica* Zone for the international boundary is the entry of *A. rotundiloba* (the "early form" of Klapper, 1985) near the base of the Frasnian Stage in southern Belgium, the region of the traditional base of the Upper Devonian (Bultynck, 1974, 1982a).

At the time the SDS was selecting the international boundary, the lowest-known occurrences of *Ancyrodella rotundiloba* in New York, apart from the Leicester Pyrite and North Evans Limestone at the boundary unconformity in the western part of the state, were reported by Huddle (1981) from several levels in the middle of the grey Penn Yan Shale between the Genesee Valley and Canandaigua Lake (Kirchgasser, 1985). In that region, specimens referred to as the "early form" of *A. rotundiloba* sensu Klapper (1985) were subsequently found in a horizon in the Honeoye Valley only 2.0 m above the base of the Penn Yan Shale (Kirchgasser et al., 1986). From even lower in the Penn Yan Shale in the same area, the "early" and "late" forms of *A. rotundiloba* were identified in horizons of reworked pyrite and phosphate debris 15–60 cm above the main bed of the Lodi Limestone (Baird et al., 1989; Kirchgasser et al., 1988, 1989; Figures 1–3). In the Bristol and Canandaigua Valleys a few kilometers east of the Honeoye Valley, where the Lodi Limestone has been cut out by submarine erosion, the horizon with the lowest occurrence of *A. rotundiloba* (and the Middle–Upper Devonian boundary) is at the base of the Penn Yan Shale at its contact with the underlying Genesee Shale. All of the lower Penn Yan Shale occurrences of *A. rotundiloba* are here regarded as early morphotypes of the species. They correlate with the Lower *asymmetrica* Zone, the base of which is the SDS Middle–Upper Devonian boundary, and Montagne Noire Zone I of Klapper (1989) and Klapper and Johnson (1990).

Since the boundary-defining occurrences of *Ancyrodella rotundiloba* in New York were first reported, fundamental disagreements over the taxonomy of the species have arisen (Sandberg et al., 1988, 1989; Klapper, 1988). In addition, the suitability of species of *Ancyrodella* as zone fossils for intercontinental correlation has been questioned, in part because of their presumed restriction to neritic biofacies (Bultynck, 1986; Sandberg et al., 1988, 1989; Racki and Wrzolek, 1989). As a con-

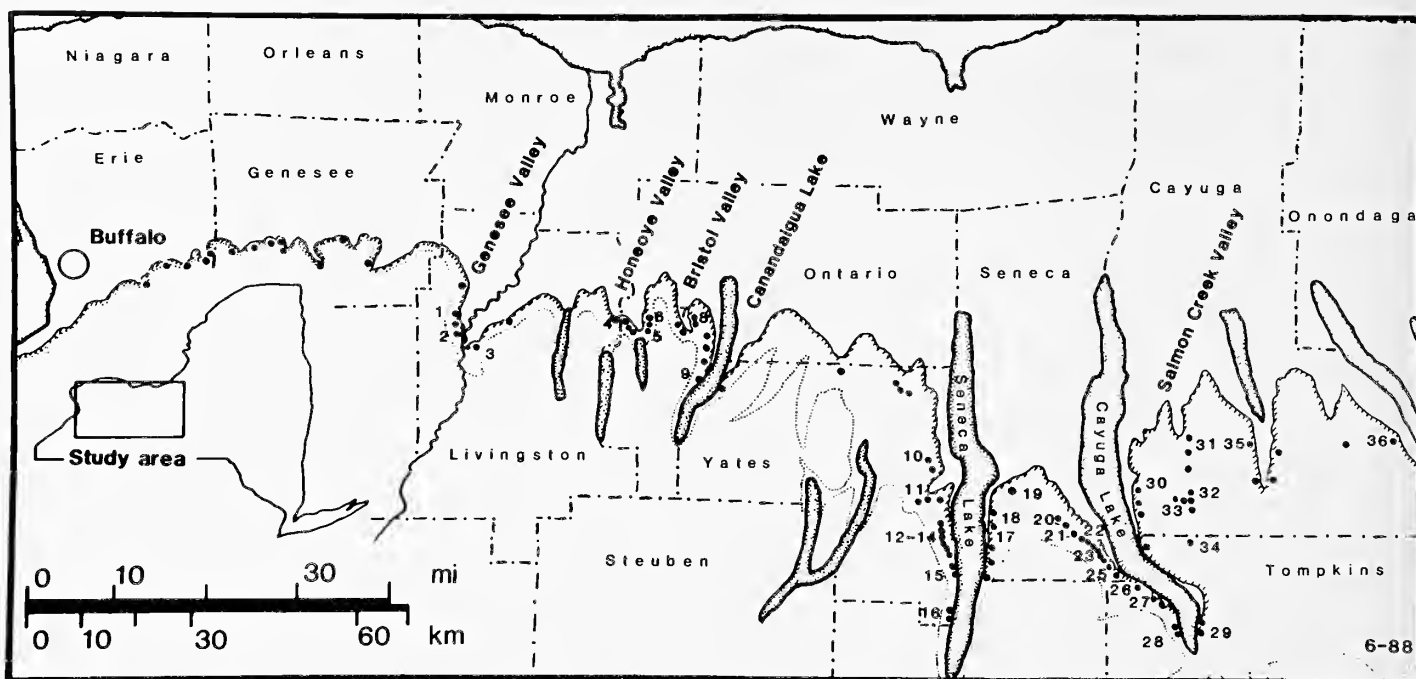


Figure 1. Locality map of area of study. Dot-dash lines are county lines. Hachured and dotted lines denote base and top, respectively, of the Genesee Formation. From Baird et al. (1989) and Kirchgasser et al. (1989). Locality details are given in these publications and in Appendix 1.

sequence, a major revision of the standard zonation has been proposed (Sandberg et al., 1989). The purpose of this paper is to document the *Ancyrodella* and subjacent faunas reported earlier from New York in light of these developments.

Status of *Ancyrodella rotundiloba* and the Middle–Upper Devonian boundary

Earlier reports

The central issue concerning *Ancyrodella rotundiloba* as the boundary-defining taxon is whether the morphotype referred to as the “early form” of *Ancyrodella rotundiloba* by Klapper (1985) belongs to *Ancyrodella rotundiloba* (Bryant, 1921). Sandberg et al. (1988, 1989) argued that Klapper’s “early form” does not belong to *A. rotundiloba*, but instead represents phylogenetically earlier forms (i.e., *A. pristina* Khalymbadzha and Chernysheva, 1970, and *A. soluta* Sandberg, Ziegler, and Bultynck, 1989) that descended from ancestral *A. binodosa* Uyeno (1967). As a consequence, they claimed that the GSSP (CPS-E, Bed 42a) is not at the intended level at the base of the Lower *asymmetrica* Zone, but rather at an undefined position within the underlying Lowermost *asymmetrica* Zone. They drew the Lower *asymmetrica* boundary at Bed 46, where the “late form” of *A. rotundiloba* of Klapper (1985) has its lowest local occurrence. Following a similar argument, Racki and Wrzolek (1989, p. 233, fig. 1) proposed to move the GSSP upward to Bed 46 where, in their view, the “true” *A. rotundiloba* (and Lower *asymmetrica* Zone) begins.

In preparing his response to Sandberg et al. (1988), Klapper re-examined Bryant’s types from the North Evans Limestone and confirmed the presence of the “early form” of *Ancyrodella rotundiloba* among the paralectotypes. This reinforced his earlier conclusion (Klapper, 1985, p. 26) and the traditional usage (see species synonymy

in Klapper, 1985, and reports in Ziegler and Werner, 1986) that the “early form” of *A. rotundiloba* is within the range of variability of the species (Klapper, 1988, p. 180). In a separate response to Sandberg et al. (1988), Johnson (1988) noted that Klapper’s recognition of the “early form” of *A. rotundiloba* as a member of the species was anticipated by earlier workers, who also included it in the species. A critical example cited by Johnson (1988) was Bultynck’s (1982b, Pl. 1, figs. 26–27) assignment of the “early form” of Klapper (1985) to *A. rotundiloba* in Bed 41 in the section at Nismes, Belgium. This particular occurrence of *A. rotundiloba* above Givetian-age beds with *A. binodosa* is significant because it is near the traditional Givetian–Frasnian Stage boundary in the type area of the Frasnian Stage (Bultynck, 1982a, 1982b). This occurrence was one of the compelling reasons behind the SDS decision to select the entry of *A. rotundiloba* and the Lower *asymmetrica* boundary as the Stage and Series boundary.

By assigning the “early form” of *Ancyrodella rotundiloba* of Klapper (1985) to *A. pristina* and *A. soluta*, and by including representatives of *Ancyrodella alata* Glenister and Klapper (1966) and *A. rugosa* (Branson and Mehl, 1934) in their concept of *A. rotundiloba* (see below), Sandberg et al. (1989) effectively removed all morphotypes from Bryant’s species, with the exception of the “late form” as represented by the lectotype. In addition, Sandberg et al. (1989) concluded that *Ancyrodella* and *Skeletognathus* were neritic and facies-controlled, and that such biofacies-restricted genera were not suitable for zonations and correlations beyond local areas. They proposed a revised standard zonation around the Middle–Upper Devonian boundary in which the traditional Lowermost *asymmetrica* and Lower *asymmetrica* Zones, defined in part by such supposed neritic species as *Skeletognathus norrisi* and *A. rotundiloba*, were replaced by a sequence based on species of the pelagic genera *Mesotaxis* and *Palmatolepis*. None of the boundaries in their new zonation are at or near the position of the SDS Middle–Upper Devonian boundary (Sandberg et al., 1989, fig. 1). The lowest, or *falsiovalis* Zone,

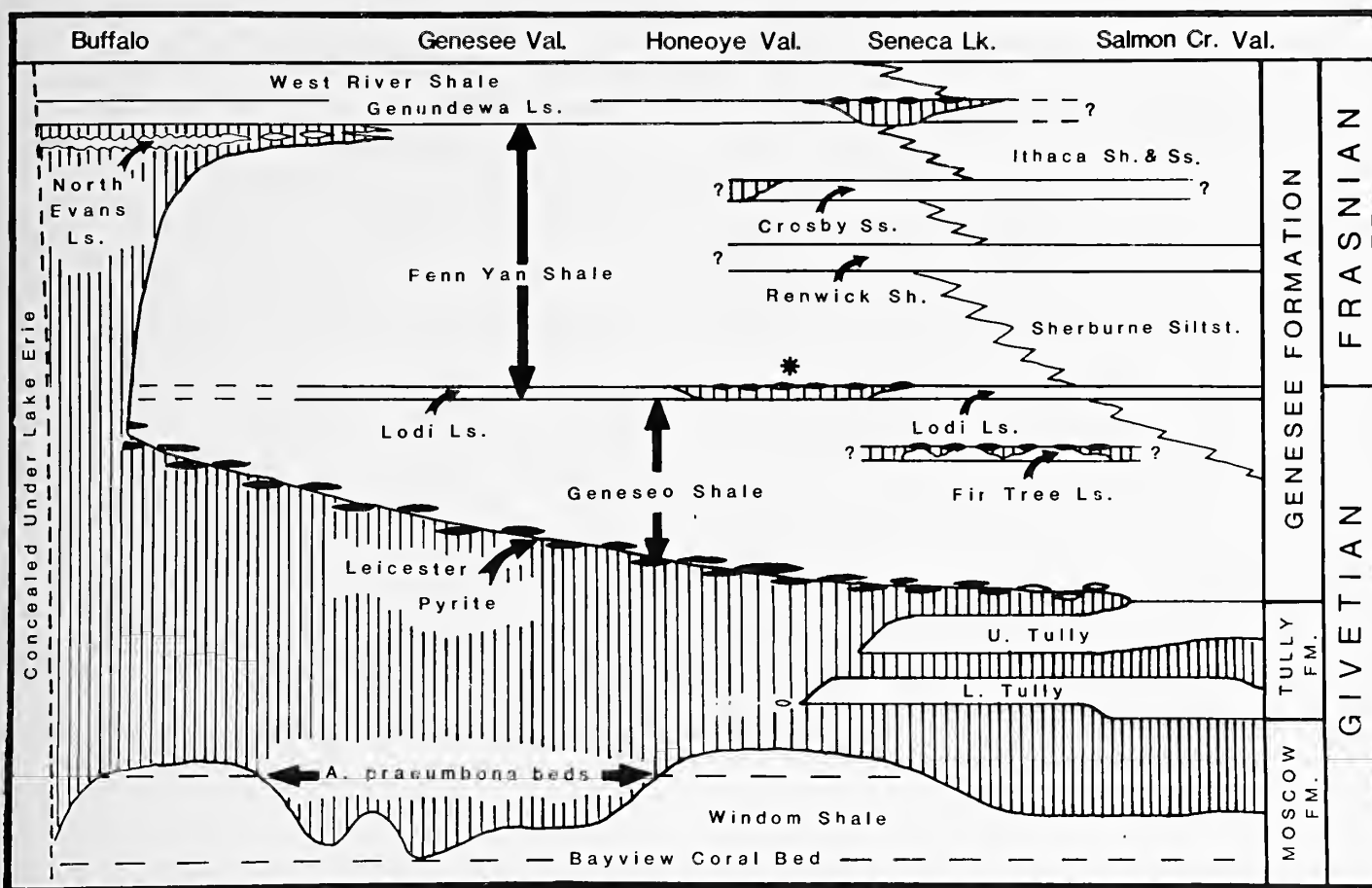


Figure 2. Cross-section of lower Genesee Formation and adjacent units showing key conodont horizons around the Givetian–Frasnian (Middle–Upper Devonian) boundary. Note position of locally bevelled Fir Tree and Lodi Limestones in the Honeoye Valley–Seneca Lake region. Asterisk indicates discontinuity-horizon with lowest occurrence of *Ancyrodella rotundiloba* (early morphotype) at the Middle–Upper Devonian boundary. From Kirchgasser et al. (1989), after Baird and Brett (1986b).

named for *Mesotaxis falsiovalis* Sandberg, Ziegler, and Bultynck, 1989, spans the interval of the Lowermost *asymmetrica* and most of the Lower *asymmetrica* Zones. Klapper and Johnson (1990) regarded *Mesotaxis falsiovalis* as a morphotype within the species *Mesotaxis asymmetrica* (Bischoff and Ziegler), and one not deserving even of subspecies rank. In rejecting the *falsiovalis* Zone, Klapper and Johnson (1990) proposed the *norrisi* Zone as the terminal Middle Devonian conodont zone. A few fragments of possible *Mesotaxis asymmetrica* have been noted in the Lodi Limestone, but the lowest locally occurring undoubted representatives of *M. asymmetrica* and the related *Mesotaxis ovalis* (Ziegler and Klapper, 1964 [= *Polygnathus unilabius* Huddle, 1981]) in west-central New York occur in the West River Shale in the upper Genesee Formation.

Klapper has continued to refine the sequence of *Ancyrodella* species in the lower Frasnian. Klapper (1989), Klapper and Lane (1989), and Klapper and Johnson (1990) also abandoned the traditional zonation of the lower Frasnian and proposed a zonation based, in the lower part, on the sequence in the Montagne Noire. Four numbered zones, the lowest three based on the lowest local occurrence of morphotypes of species of *Ancyrodella*, subdivide the traditional Lower *asymmetrica* Zone. The lowest occurrence of the “early form” of *A. rotundiloba* of Klapper (1985) (=early morphotype of *A. rotundiloba* as interpreted herein) defines the base of Montagne Noire Zone 1 of Klapper and Johnson

(1990) and the base of the Upper Devonian.

In revising the uppermost Middle Devonian conodont zones, Klapper and Johnson (1990, p. 934–935, fig. 52) proposed the *norrisi* Zone (as a substitute for the Lowermost *asymmetrica* Zone) for the terminal Middle Devonian zone below Montagne Noire Zone 1, with the base of the *norrisi* Zone defined on the lowest occurrence of *Skeletognathus norrisi* with *Pandorinellina insita* and *Mesotaxis asymmetrica* s.l. They also formally subdivided the *disparilis* Zone, with the base of the Upper *disparilis* Subzone defined at the lowest occurrence of *Polygnathus dengleri* and the top of the Upper *disparilis* Subzone defined by the lowest occurrence of *S. norrisi*. In the revised zonation of Klapper and Johnson (1990), the Fir Tree Limestone of the upper Genesee Shale correlates (tentatively) with the Upper *disparilis* Subzone; the Lodi Limestone correlates with the *norrisi* Zone; and the lower Penn Yan Shale, with the early morphotype of *A. rotundiloba*, correlates with Montagne Noire Zone 1 (Figure 4).

Discussion

Wide variation has long been recognized in *Ancyrodella rotundiloba* (Müller and Clark, 1967; Ziegler, 1973; Klapper, 1985), particularly in the shape of the platform; the development of lobes; the size and shape of the pit; the development of incipient keels; and the number, size, and pattern of the nodes on the upper surface. The subspecies *A. rotundiloba*

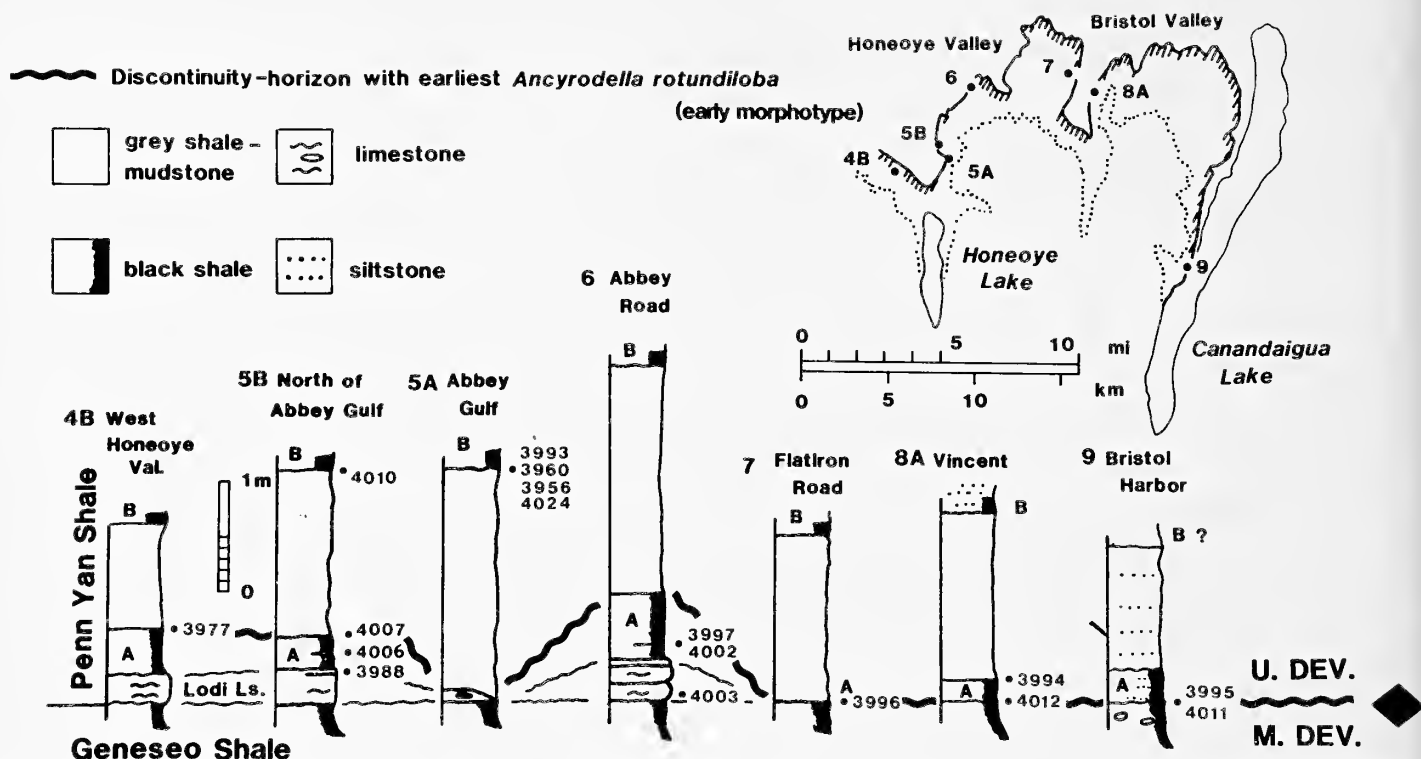


Figure 3. Detail of sections around the Middle-Upper Devonian boundary between the Honeoye and Canandaigua Lake Valleys showing sample numbers and discontinuity horizon with earliest *Ancyrodella rotundiloba* (early morphotype).

SYSTEM	STAGE	MIDDLE				UPPER DEVONIAN																
		GIVETIAN				FRASNIAN																
CONODONT ZONES	1		<i>disparilis</i> ?U			Lm	<i>asymmetrica</i> Lower															
	2		?U <i>disparilis</i> Subz.			<i>norrissi</i>	M.N. 1				M.N. 2				M.N. 3							
UNITS	TULLY LS / WINDOM SHALE	GENESEE FORMATION																				
		GENESEO SHALE				PENN YAN SHALE												GENUNDEWA LIMESTONE		WEST RIVER SHALE		
						LODI LS																
		LP			FT	A	B	A	B	REN	SB	FBS	LH	CSS		L	U					
<i>Icriodus symmetricus</i> s. l.		X	X	X		X	X	X	X			X		X	X							
<i>Polygnathus dubius</i> s. l.		X	X	X	X	X	X	X	X			X		X	X	X						
<i>Schmidognathus peracutus</i>		X	X		?sp																	
<i>Polygnathus? caelatus</i>		X	X	X		X	X	X														
<i>P. ordinatus</i>		X	X	X								?										
<i>P. cristatus</i>		X										?										
<i>P. alatus</i>		X										X		X	X	X						
<i>Palmatolepis disparalvea</i>		X					X		X													
<i>Polygnathus pennatus</i>					?	X	X	X	X			X		X	X	X						
<i>Palmatolepis disparilis</i>					?																	
<i>Polygnathus dengleri</i>					?	X	X	?	X			X		X	X	X						
<i>Mesotaxis asymmetrica</i>								?									X					
<i>Skeletognathus norrisi</i>						X	X															
<i>Polygnathus cristatus?</i> s. Klapper, 1989.						X	X		X													
<i>Ancyrodella rotundiloba</i> (early morph.)								X	X			X		X								
<i>A. rotundiloba</i> (late morph.)														X	X	X						
Conodont faunas		<i>Polygnathus ordinatus</i>				Skel. <i>norrissi</i>		<i>Ancyrodella rotundiloba</i> (early morphotype)						<i>A. rotundiloba</i> (late morphotype)				<i>A. alata</i>				
AMMONOID SEQUENCE		1	<i>Pharciceras</i>																<i>Manticoceras</i>			
		2	? <i>Pharciceras</i>				<i>Ponticeras</i>						<i>Proboloceras</i> & <i>Koenenites</i>						<i>Mant.</i>			
3-91		3	<i>Phar.</i> & <i>Ponticeras</i> .				<i>Proboloceras</i> & <i>Petteroceras</i>						<i>Koen.</i>									

Figure 4. Distribution of key conodonts in the lower Genesee Formation between the Genesee and Salmon Creek Valleys. Data for the Leicester Pyrite and lower Genesee Shale from Huddle (1981); data from sections west of the Genesee Valley not included. Conodont Zones: 1. Standard Zonation; 2. Revised zonation of Klapper (1989) and Klapper and Johnson (1990) (M.N.=Montagne Noire Zones). Stratigraphic terminology after deWitt and Colton (1978), Baird et al. (1989), and Kirchgasser et al. (1989). Abbreviations of units: LP (Leicester Pyrite), LG (lower Genesee), FT (Fir Tree Limestone [Baird and Brett, 1986b]), A (basal) and B (main) beds of the Lodi Limestone (Kirchgasser et al., 1989), A, B (Black shales A and B of the base and lower part, respectively, of the lower Penn Yan Shale [Kirchgasser et al., 1986, 1989]), REN (Renwick Shale), SB (SB Black Shale [Kirchgasser et al., 1986]), FBS (Firestone Beds [Kirchgasser, 1985]), LH (Linden Horizon [Kirchgasser and House, 1981]), CSS (Crosby Sandstone), L, U (Lower and Upper Genundewa Limestone [Kirchgasser et al., 1986]). Conodont faunas are assemblages named for their diagnostic species. Ammonoid Sequence: 1. Standard zones (House, 1985); 2. New York generic occurrences (Kirchgasser and House, 1981); 3. Montagne Noire generic occurrences (House et al., 1985).

alata Glenister and Klapper, 1966, is now recognized as a separate and later species with distinctive platform shapes and keels (Klapper, 1985). General agreement also exists that *A. binodosa* Uyeno (1967), with its "binodose" pattern nodes and rounded anterior lobes and pit margins, is the earliest species of the genus and thus a stratigraphically lower species than *A. rotundiloba*. Bultynck and Jacobs (1981) expanded the concept of *A. binodosa* to include specimens that Klapper (1985) assigned to the "early form" of *A. rotundiloba*, although there are transitional morphotypes. The position of *A. binodosa* and the transitional morphotypes in the *norrisi* Zone of Klapper and Johnson (1990) is unclear.

Some varieties of *Ancyrodella rotundiloba* characterize particular geographic regions. In the Squaw Bay Limestone of Michigan, three varieties are differentiated on the basis of the pattern of nodes on the upper surface (Müller and Clark, 1967): normal (irregular distribution), cruciform (nodes aligned perpendicular to the carina near the anterior end of the platform), and symmetrical (rows of nodes aligned parallel to the carina). Typical specimens from the lower Penn Yan Shale in New York display the symmetrical pattern in which a row of nodes on either side of the carina converges posteriorly toward the carina and then parallels the carina. This pattern is also seen in late morphotypes, including the lectotype. In the Montagne Noire, the cruciform pattern dominates (Klapper, 1985). Wide variation is also observed among adult specimens from a single horizon or sample, as was demonstrated by Müller and Clark (1967) in the Squaw Bay Limestone and as illustrated herein by variation in specimens from the lower Penn Yan Shale (Plate 1). As a consequence of such wide geographic variation, markedly different stratigraphic sequences and phylogenies have been proposed for the early lineages of *Ancyrodella* (see Khalymbadzha and Chernysheva, 1970; Ziegler, 1962; Bultynck, 1983; Klapper, 1985, 1989; Garcia-Lopez, 1986b; and Sandberg et al., 1989). From among these sequences, the sequence in the Genesee Formation in New York is closest to that of the Montagne Noire.

In his study of *Ancyrodella* in the Montagne Noire, Klapper (1985) was the first to recognize a sequence of morphotypes within *A. rotundiloba* and *A. alata* and the possibility of using them to subdivide the Lower *asymmetrica* Zone. The stratigraphically lower "early form" of *A. rotundiloba* is distinguished from the higher-appearing "late form" by its larger and more irregular pit and fewer nodes on the upper surface of the platform. Although the lectotype of *A. rotundiloba* (Bryant, 1921) as selected by Ziegler (1958) is a "late form" of the species, Klapper (1985, 1988, 1989) maintained that the "early form" is represented among the paralectotypes and is thus within the range of variability of Bryant's species. In opposing this view, Sandberg et al. (1988, 1989) removed the "early form" of Klapper (1985) from *A. rotundiloba* and assigned some representatives to *A. pristina* Khalymbadzha and Chernysheva, 1970, and others to *A. soluta* Sandberg, Ziegler, and Bultynck, 1989. In addition, they expanded the concept of *A. rotundiloba* to include forms referable to *Ancyrodella alata* (see Klapper, 1988, p. 181; Klapper and Johnson, 1990, p. 935-936) and to *Ancyrodella rugosa*. As a consequence of these decisions, all of the specimens figured by Sandberg et al. (1989) under the name *A. rotundiloba*, with the exception of the lectotype, belong either to *A. alata* or to *A. rugosa*.

Conclusion

In the preparation of the systematic section of this paper, the specimens from the lower Penn Yan Shale were compared with the lectotype

and nine surviving paralectotypes of *Ancyrodella rotundiloba* (Bryant, 1921) from the North Evans Limestone. The specimen illustrated by Bryant (1921) as his Figure 7 is apparently lost. The remaining paralectotypes vary widely in form and are rather poorly preserved. However, Klapper's (1988) interpretation that they all belong in *Ancyrodella rotundiloba* is confirmed. One (and possibly two) of the specimens, and the specimen illustrated in Bryant's (1921) Figure 7, are early morphotypes, and are similar to the lower Penn Yan Shale specimens and the "early form" of Klapper (1985) from the Montagne Noire. Although distinctions can be made among the various early morphotypes of *A. rotundiloba*, it seems ill-advised to name each type formally until the other elements of the apparatuses are identified and described, and until the biostratigraphic sequence is confirmed independently through correlations that use other groups.

The informal designation "early morphotype" is employed herein for morphotypes in the early evolution of *Ancyrodella rotundiloba*, including the "early form" of Klapper (1985) and *A. pristina* and *A. soluta* (see synonymy). Similarly, the designation "late morphotype" refers to later morphotypes of *A. rotundiloba* in the interval between the lowest local occurrence of the early morphotype and the lowest local occurrence of *Ancyrodella alata*. Included in the late morphotype of *Ancyrodella rotundiloba* are the lectotype, seven or eight of Bryant's paralectotypes, and the "late form" of Klapper (1985) from the Montagne Noire.

Future usage will, of course, determine the fate of Bryant's species *Ancyrodella rotundiloba* and the boundary stratotype defined on its first occurrence. Whatever names are used for the early and late morphotypes of *A. rotundiloba*, the available evidence from the Montagne Noire and North America suggests that these morphotypes, as well as other supposed neritic taxa such as *Skeletognathus* and *A. alata*, occur in a sequence that permits correlation at a higher level of resolution than has been possible with either the old standard conodont zonation or the revised zonation of Sandberg et al. (1989; Klapper, 1989; Klapper and Lane, 1989; Klapper and Johnson, 1990). Comparison of the ammonoid sequences in New York and the Montagne Noire generally supports the conodont correlations, but major gaps exist, and the boundaries of generic ranges do not precisely coincide (Figure 4).

The sporadic occurrences of conodonts and ammonoids in the Genesee Formation reflect a complex pattern of facies shifts caused by eustatic sea-level fluctuation (House, 1985), episodic Acadian uplifts (Ettensohn, 1985), and changes in taphonomic conditions as modelled by Baird and Brett (1986a, 1986b) and Baird et al. (1989). In such discontinuous faunal successions, the lowest local occurrences of taxa, whether neritic or pelagic, are likely to be "cryptogenic" and "biofacies" lowest occurrences, to use the terminology of Sandberg et al. (1988, p. 117). In spite of these limitations, however, the order of lowest occurrences in New York appears to have been preserved, at least when compared to the sequence recorded in the comparatively continuous succession of pelagic limestones in the Montagne Noire (Feist and Klapper, 1985). Of course, the precise position of the local lowest (or highest) occurrences of morphotypes of *Ancyrodella* and other taxa in New York (and elsewhere) relative to their total or global ranges can be determined only when the ranges of all known occurrences have been correlated into composite ranges, a task that G. Klapper (personal commun.) has undertaken for the Frasnian Stage by the use of graphic correlation. Certainly no claim is made herein that the base of the Penn Yan Shale corresponds to the lowest global occurrence of the early morphotype of *A. rotundiloba*. A study of lower Upper Devonian conodont and goniatite sequences currently underway in the Canning Basin

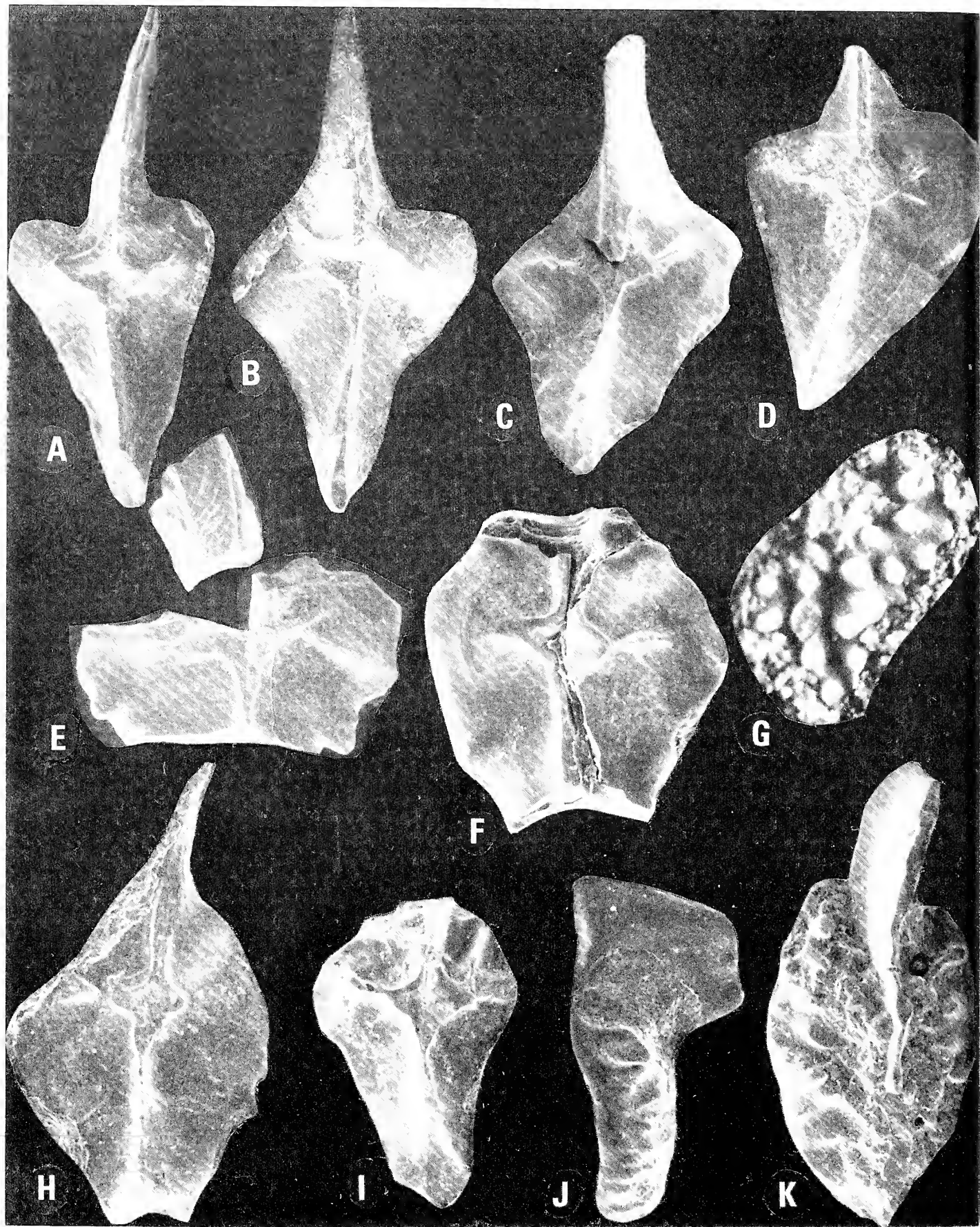


Plate 1. *Ancyrodella rotundiloba* (Bryant) (early morphotypes) and *Polygnathus? caelatus* Bryant from basal and lower Penn Yan Shale, Genesee Formation, west-central New York. Magnifications all x60; all figures are Pa elements. *A-I*, *Ancyrodella rotundiloba* (Bryant). *A*, lower view of USNM 453926, Sample 4012, base of Black shale A at base of Penn Yan Shale, Loc. 8A, tributary to Mud Creek, 0.7 km northeast of Vincent, Ontario County (Bristol Valley); *B-D*, lower views of *B*, USNM 434051; *C*, USNM 434053; *D*, USNM 434050, Sample 3994, top of Black shale A, lower Penn Yan Shale, Loc. 8A, tributary to Mud Creek, 0.7 km northeast of Vincent, Ontario County (Bristol Valley); *E-F*, lower views of *E*, USNM 434054; *F*, USNM 434055, Sample 3995, base of Black shale A at base of Penn Yan Shale, Loc. 9, base of cliff below Bristol Harbor condominiums, west shore of Canandaigua Lake, Ontario County; *G*, upper view showing nodes at posterior end of platform of USNM 453924, Sample 3996, Black shale A at contact of Genesee and Penn Yan Shales, Loc. 7, tributary to Mud Creek adjacent to Flatiron Road, 1.3 km northeast of Bristol, Ontario County (Bristol Valley); *H*, lower view of USNM 453925, Sample 4007, top of Black shale A, lower Penn Yan Shale, Loc. 5B, gully 0.5 km north of Abbey Gulf, 2.9 km northeast of Honeoye, Ontario County (Honeoye Valley); *I*, lower view of USNM 434040, Sample 3977, top of Black shale A, lower Penn Yan Shale, Loc. 4B, west side of Honeoye Valley, 2.1 km northwest of Honeoye, Ontario County (Honeoye Valley). *J-K*, *Polygnathus? caelatus* Bryant. *J*, lateral view of USNM 434052, Sample 3994, top of Black shale A, lower Penn Yan Shale, Loc. 8A, tributary to Mud Creek, 0.7 km northeast of Vincent, Ontario County (Bristol Valley); *K*, upper view of USNM 453923, Sample 3996, Black shale A at contact of Genesee and Penn Yan Shales, Loc. 7, tributary to Mud Creek adjacent to Flatiron Road, 1.3 km northeast of Bristol, Ontario County.

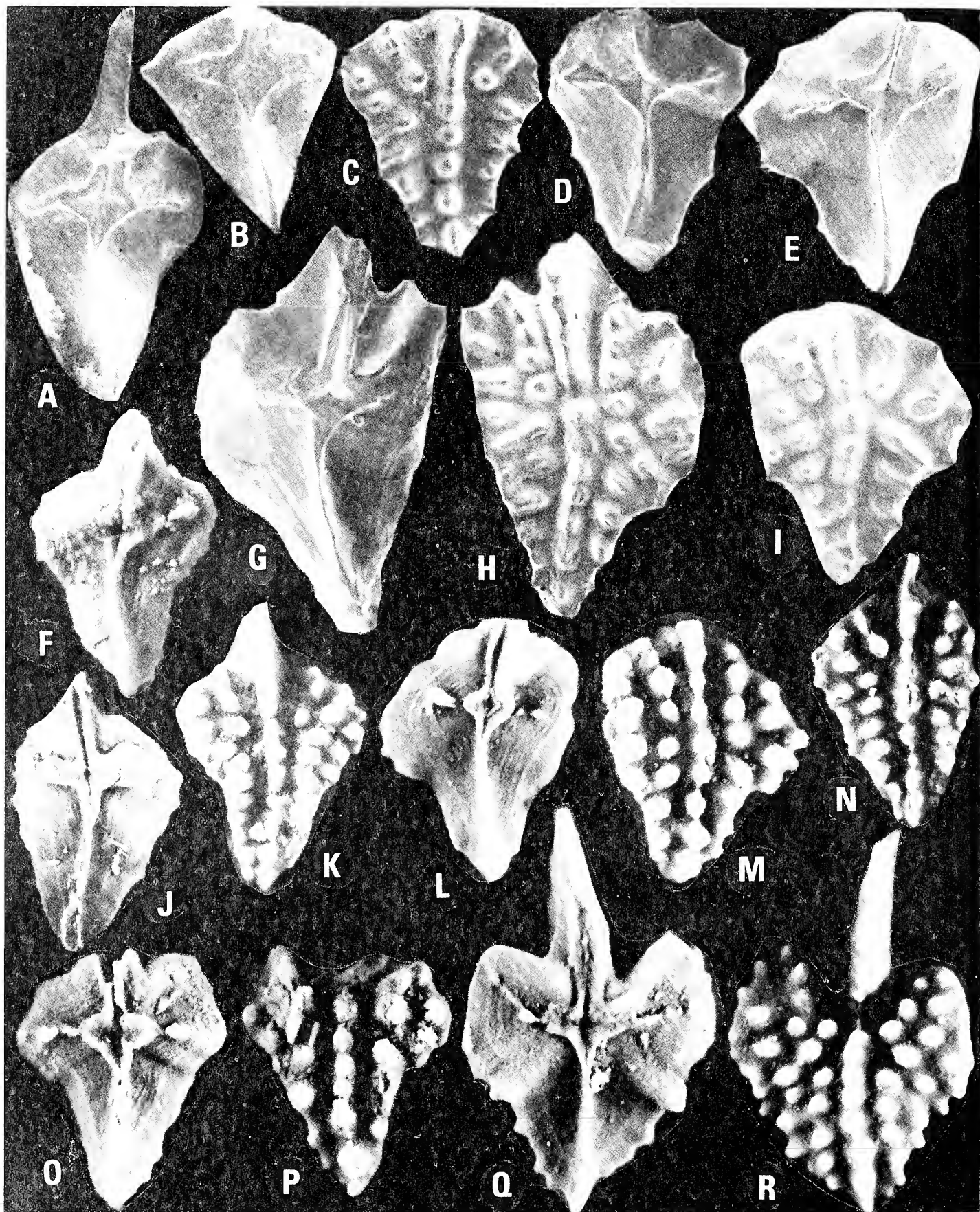


Plate 2. *Ancyrodella rotundiloba* (Bryant) (early and late morphotypes) from Penn Yan Shale and equivalents, Genesee Formation, west-central New York. All figures are Pa elements. *A-K, N-P, Ancyrodella rotundiloba* (Bryant) (early morphotype). *A*, lower view of USNM 434033, Sample 3960; *B*, lower view of USNM 434034, Sample 3960; *C-D*, upper and lower views of USNM 453929, Sample 4024; *E, I*, lower and upper views of USNM 453928, Sample 4024; *G-H*, lower and upper views of USNM 453927, Sample 4024, base of Black shale B (horizon 21/1c of Kirchgasser et al., 1986), lower Penn Yan Shale, Loc. 5A, main section in Abbey Gulf, 2.6 km northeast of Honeoye, Ontario County (Honeoye Valley) (*A* and *B* in sample with goniatite *Ponticeras perlatum* Hall), x60; *F, K*, lower and upper views of USNM 434032, Sample 3957, SB Black Shale (Kirchgasser et al., 1986, p. 249, 251), Penn Yan Shale, 5.2 m above western nodule bed of the Lodi Limestone at base of section, Dewey Hill roadcut (south side of Rte. 39-20A), 2.0 km southwest of Geneseo, Livingston County (Genesee Valley) (photograph by J. Kralick), x50; *J, N*, lower and upper views of USNM 434031, from limestone sample with ammonoid *Ponticeras* s.p. cf. *regale* (Holzapfel), New York State Museum 3753, Firestone Beds (FBS), Ithaca shale and sandstone, Genesee Formation, Fall Creek, Ithaca, Tompkins County (Cayuga Valley) (Loc. DY-10 of deWitt and Colton, 1978; Kirchgasser, 1985, fig. 5), x40; *O, P*, lower and upper views of USNM 453930, Sample 11/1c, 1.6 to 3.2 cm above base of North Evans Limestone, Genesee Formation, creek level, 125 m west of railroad bridge, Eighteenmile Creek, 1.1 km northwest of North Evans, Erie County, x50. *L, M, Q, R, Ancyrodella rotundiloba* (Bryant) (late morphotypes). *L, M*, lower and upper views of USNM 434030 (morphotype in Crosby Sandstone recognized by Klapper, 1985); *Q, R*, lower and upper views of USNM 434029, Sample 3881, Crosby Sandstone (CSS), Penn Yan Shale, Sunset Point gully, 9.3 km southwest of Penn Yan, Yates County (Keuka Lake) (Loc. Py-16 of deWitt and Colton [1978]; horizon at lowest occurrence of goniatite *Koenenites styliophilum* [Clarke]), x60.

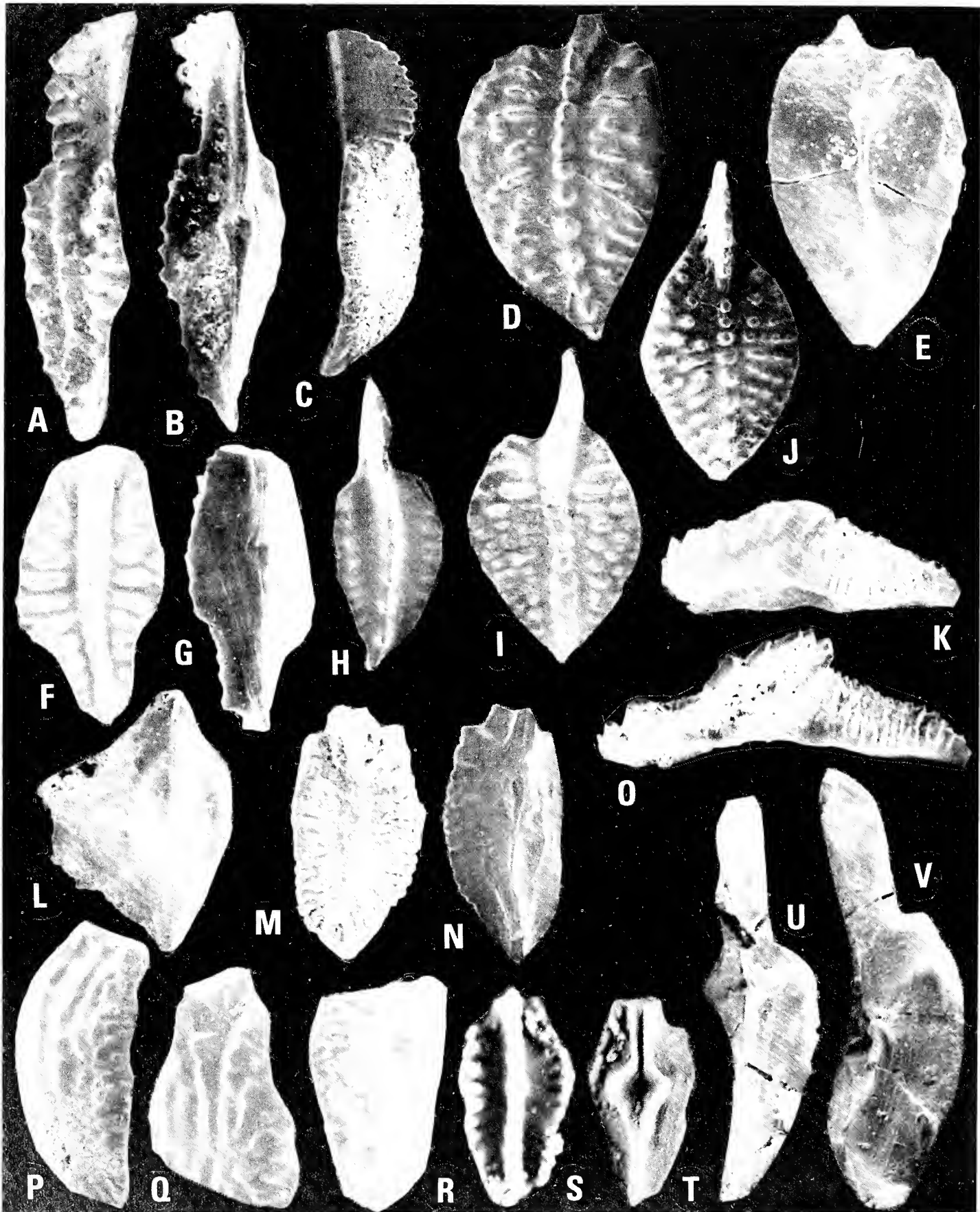


Plate 3. Conodonts from Fir Tree Limestone (FT) of upper Genesee Shale and Lodi Limestone of lower Penn Yan Shale and lower Sherburne Siltstone, Genesee Formation, west-central New York. All figures are Pa elements unless noted otherwise.

A, B, F, G, Polygnathus pennatus Hinde. *A, B*, oblique upper view and lower view of USNM 434038, Sample 3971, western nodule bed of Lodi Limestone, Loc. 3, Fall Brook, 2.4 km south of Genesee, Livingston County (Genesee Valley), x60; *F, G*, upper and lower views of USNM 434027, Sample 3013, Bed B of Lodi Limestone, Loc. 17, Mill Creek (Lodi Glen), 3.0 km west of Lodi, Seneca County (Seneca Lake Valley) (type horizon and locality of ammonoid *Ponticeras perlatum* [Hall]), x50.

C, K, M, N, O, Skeletognathus norrisi (Uyeno). *C*, oblique upper view of USNM 434035, x50; *O*, oblique lateral view of Pb element, USNM 434036, Sample 3969, x60, western nodule bed of Lodi Limestone, Loc. 1, Taunton Gully, 2.7 km north of Leicester, Livingston County (Genesee Valley); *K*, oblique lateral view of Pb element, USNM 434045, Sample 3979, x60; *M, N*, upper and lower views USNM 434047, Sample 3979, x70, Bed A of Lodi Limestone, base of Penn Yan Shale or Sherburne Siltstone at contact with Genesee Shale, Loc. 17, Mill Creek (Lodi Glen), 3.0 km west of Lodi, Seneca County (Seneca Lake Valley).

D, E, I, J, Polygnathus cristatus? Hinde (sensu Klapper, 1989). *D, E*, upper and lower views of USNM 434039, Sample 3971a, x60; *J*, upper view of USNM 434037, Sample 3971, x70, western nodule bed of Lodi Limestone, Loc. 3, Fall Brook, 2.4 km south of Genesee, Livingston County (Genesee Valley); *I*, upper view of 434026, Sample 3013, x50, base of Bed B of Lodi Limestone, lower Penn Yan Shale or Sherburne Siltstone, Loc. 17, Mill Creek (Lodi Glen), 3.0 km west of Lodi, Seneca County (Seneca Valley).

H, Polygnathus dengleri Bischoff and Ziegler. Upper view of USNM 434028, Sample 3013, Bed B of Lodi Limestone, lower Penn Yan Shale or Sherburne Siltstone, Loc. 17, Mill Creek (Lodi Glen), 3.0 km west of Lodi, Seneca County (Seneca Valley), x70.

L, Palmatolepis disparalvea Orr and Klapper. Lower view of USNM 434046, Sample 3979, Bed A of Lodi Limestone, base of Penn Yan Shale or Sherburne Siltstone at contact with Genesee Shale, Loc. 17, Mill Creek (Lodi Glen), 3.0 km west of Lodi, Seneca County (Seneca Valley), x50.

P-R, Polygnathus ordinatus Bryant. *P*, oblique view of upper side of USNM 434043, x40; *Q*, oblique view of upper side of USNM 434042, Sample 3978, pyrite bed of Fir Tree Limestone, Loc. 32, tributary to Big Salmon Creek, Genoa, Cayuga County, x50; *R*, upper view of USNM 434048, Sample 3989, pyrite bed of Fir Tree Limestone, Loc. 31, tributary to Big Salmon Creek, 1.1 km northeast of Venice Center, Cayuga County, x50.

S-V, Schmidtognathus? sp. *S, T*, upper and lower views of USNM 434049, Sample 3989, pyrite bed of Fir Tree Limestone, Loc. 31, tributary to Big Salmon Creek, 1.1 km northeast of Venice Center, Cayuga County, x50; *U*, oblique view of lower side of USNM 434044, x50; *V*, oblique view of lower side of USNM 434041, Sample 3978, pyrite bed of Fir Tree Limestone, Loc. 32, tributary to Big Salmon Creek, Genoa, Cayuga County, x50.

of Western Australia by G. Klapper, M.R. House, R.T. Becker, and W.T. Kirchgasser will provide an independent test of the correlations between New York and the Montagne Noire, and will determine whether species of *Ancyrodella* are useful for intercontinental, high-resolution correlations through the Middle–Upper Devonian boundary.

Stratigraphy and samples

The conodont horizons reported herein were discovered during a collaborative study of the stratigraphy of the lower Genesee Formation with G.C. Baird and C.E. Brett. Baird and Brett discovered that limestones, when traced basinward, pass into discontinuity horizons of reworked pyrite, quartz sand, and phosphate debris that are capped by black shale (Brett and Baird, 1982; Baird and Brett, 1986a, 1986b; Figure 2). These lag deposits, which include bedding-plane surfaces with conodont elements, remained after the carbonate was removed by submarine solution and scour in marginally dysoxic and anoxic water. The facies changes from limestone to pyrite for the Fir Tree Limestone (Baird and Brett, 1986b) and Lodi Limestone were described in Baird et al. (1989) and Kirchgasser et al. (1989).

The general stratigraphic terminology for the Genesee Formation is modified from deWitt and Colton (1978), in which the principal units (e.g., Lodi Limestone and Penn Yan Shale) are regarded as members of the formation. Sources of the names and abbreviations of key lithic and faunal horizons are given in the explanation of Figure 4, in Baird et al. (1989) and Kirchgasser et al. (1989), and in references therein.

Locations of conodont samples from the Lodi Limestone and lower Penn Yan Shale in the Honeoye to Canandaigua region are shown in Figure 3. The locality details for all samples are given in the Appendix.

Conodont elements were recovered by standard acid etching of carbonates, or were found concentrated with residual pyrite and phosphate debris on the surfaces of black shales. Most specimens on the bedding-plane surfaces are broken, and the lower side is typically exposed. Some success was achieved in freeing specimens from the black shale with household bleach (sodium hypochlorite), but in most cases the upper sides remained covered with attached sediment. Work is continuing higher in the Penn Yan Shale, and J. Kralick is studying the sequence of *Ancyrodella* species from the Crosby Sandstone to the Genundewa Limestone. A collaborative study with G. Klapper on the conodonts of the West River Shale is in progress.

Conodont sequence of the lower Genesee Formation

The range chart in Figure 4 is modified from Kirchgasser et al. (1989). Included are Huddle's (1981) data from the lower Genesee Shale and underlying Leicester Pyrite in the region of the Genesee Valley and eastward. Not included are data from west of the Genesee Valley, where the Genesee and Penn Yan Shales thin and converge at the Taghanic Unconformity. In the Lake Erie region, the base of the Genesee Formation is locally represented by the lag deposits of the Leicester Pyrite and North Evans Limestone. In these units, the biostratigraphic relations around the Middle–Upper Devonian boundary are obscure (Figure 2). Huddle (1981) and Brett and Baird (1982) demonstrated that the Leicester Pyrite is older than the North Evans Limestone, but both the "early" and the "late" morphotypes of *Ancyrodella rotundiloba* occur together in these units, and this places

both morphotypes in the lower part of the Upper Devonian (see "Systematic paleontology" below). *Ancyrodella binodosa* and transitional forms between *A. binodosa* and early morphotypes of *A. rotundiloba* are so far unknown in New York.

The Polygnathus ordinatus fauna (?Upper *disparilis* Subzone)

A fauna with *Polygnathus ordinatus* Bryant, *P.?* *caelatus* Bryant, *P. dubius* Hinde s.l., *P. dengleri* Bischoff and Ziegler, *P. pennatus* Hinde, *Palmatolepis disparilis* Ziegler and Klapper, and *Schmidtognathus?* sp. occurs in pyritic lenses that cap the Fir Tree Limestone of the upper Genesee Shale in the Salmon Creek and Cayuga Valleys. This association is questionably referable to the Upper *disparilis* Subzone of Klapper and Johnson (1990), which is defined at the lowest local occurrence of *P. dengleri*. This biostratigraphic correlation is tentative, because the records of *Polygnathus pennatus*, *P. dengleri*, and *Palmatolepis disparilis* are based on single fragments and uncertain identifications. Undoubted specimens of *P. dengleri*, *P. pennatus*, and *Palmatolepis disparalvea* Orr and Klapper, a *disparilis*-group species, occur above the Genesee Shale at the base of the Lodi Limestone (Bed A) in a fauna with *Skeletognathus norrisi* that correlates with the *norrisi* Zone of Klapper and Johnson (1990) (=Lowermost *asymmetrica* Zone). Assignment of the whole of the Genesee Shale to the *disparilis* Zone is supported by the occurrence of *Palmatolepis disparalvea* in the Leicester Pyrite immediately beneath the Genesee Shale in the Genesee Valley (Huddle, 1981).

The Skeletognathus norrisi fauna (*norrisi* Zone=Lowermost *asymmetrica* Zone)

A fauna with *Polygnathus pennatus* Hinde, *P. cristatus?* Hinde, and *Skeletognathus norrisi* (Uyeno) occurs in the Lodi Limestone (Beds A and B) at its type locality at Seneca Lake and in the western nodular bed of the Lodi Limestone in the Genesee Valley. The lowest occurrence of the distinctive species *S. norrisi* defines the base of the *norrisi* Zone of Klapper and Johnson (1990), which is equivalent to the Lowermost *asymmetrica* Zone. *Polygnathus pennatus* and the ubiquitous *P. dubius* are locally abundant in the Lodi Limestone.

Rare and poorly preserved specimens referred with question to *Mesotaxis asymmetrica* (Bischoff and Ziegler) recently have been noted in the basal bed of the Lodi Limestone (Bed A) at Seneca Lake. These problematic specimens may be *P. dengleri*, a species that certainly enters in the Lodi Limestone and occurs in most faunas up to the top of the Genesee Formation. *Mesotaxis asymmetrica* and the related *M. ovalis* (Ziegler and Klapper, 1964; =*Polygnathus unilabius* Huddle, 1981), on the other hand, do not occur with certainty in west-central New York below the West River Shale of the upper Genesee Formation. The characteristic Pa element with a broad platform in the Lodi Limestone is referable to *Polygnathus cristatus?* Hinde; this element has node ridges in the anterior end that are intermediate in form between those of *P. cristatus* Hinde and *M. asymmetrica* (Bischoff and Ziegler). *Polygnathus cristatus?* Hinde, illustrated in Klapper (1989, pl. 3, fig. 14) and herein on Plate 3, Figures D, E, I, J, ranges from the Upper *disparilis* Subzone to the lowest part of the Lower *asymmetrica* Zone in the Montagne Noire (Feist and Klapper, 1985; Klapper, 1985).

Species of the goniatites *Pharciceras* and *Ponticeras* occur in the Upper *disparilis* Subzone and *norrisi* Zone (=Lowermost *asymmetrica* Zone) in the Montagne Noire (House et al., 1985). In the equivalent interval in New York, *Pharciceras* may be represented in the upper Genesee Shale (Fir Tree Limestone), and *Ponticeras* occurs as

Ponticeras perlatum (Hall) at the top of the Genesee Shale and in the Lodi Limestone (Kirchgasser and House, 1981; Figure 4).

The Ancyrodella rotundiloba fauna (early morphotype) (lower part of Lower asymmetric Zone)

Ancyrodella rotundiloba, represented by early morphotypes of the species, appears in Honeoye Valley sections at the base of the Penn Yan Shale and immediately above the main bed of the Lodi Limestone (Bed B) (Figure 3; Locs. 4B and 5B). This key lowest occurrence is a discontinuity horizon at the top of a 0-60 cm thick black shale (Black shale A) that overlies the Lodi Limestone. In the nearby Bristol and Canandaigua Valleys, where the Lodi has been cut out, the lowest occurrences of *A. rotundiloba* are in pyrite-phosphate seams at the base and top of Black shale A at the contact between the Genesee and Penn Yan Shales (Locs. 7, 8A, 9). *Polygnathus dubius* and *P. pennatus* s.l. occur with *A. rotundiloba* in the sparse faunas at the boundary. No conodont elements were noted in the Genesee Shale immediately below. *Probeloceras* and *Petteroceras* are recorded in Zone 1 in the Montagne Noire (House et al., 1985), but only *Ponticeras* is known in the correlative interval in New York (Kirchgasser and House, 1981).

Systematic paleontology

ANCYRODELLA ROTUNDILOBA (Bryant, 1921)

Plate 1, figures A-I; Plate 2, figures A-R.

Polygnathus rotundilobus BRYANT, 1921, p. 26, 27, fig. 7 (early morphotype), Pl. 12, figs. 1-6 (late morphotype) [fig. 1=lectotype designated by Ziegler, 1958].

Ancyrodella pristina KHALYMBADZHA AND CHERNYSHEVA, 1970, p. 89-90, Pl. 1, figs. 3-8 (transitional forms between *A. binodosa* Uyeno and early morphotype of *A. rotundiloba*); SANDBERG ET AL., 1989, p. 210-211, Pl. 1, figs. 3, 4, 9, 10 (=early morphotype of *A. rotundiloba*), 13-14 (juvenile: =?early morphotype of *A. rotundiloba*).

Ancyrodella rotundiloba rotundiloba (Bryant). KHALYMBADZHA AND CHERNYSHEVA, 1970, p. 91-92, Pl. 1, figs. 9-10 (late morphotype), 11-12 (late morphotype transitional to early morphotype of *A. alata* Glenister and Klapper); HUDDLE, 1981, p. B19-20, Pl. 1, figs. 1, 2 (the lectotype [late morphotype]), 3, 6-8 (late morphotype), 11-13 (early morphotype), 14-15 (late morphotype), 16-17 (late morphotype: morphotype in Crosby Sandstone recognized by Klapper, 1985, p. 26) [not figs. 4, 5 =*A. alata*], Pl. 3, figs. 20-21 (late morphotype); BULTYNCK AND JACOBS, 1981, p. 17, 18, Pl. 10, ?figs. 1-3 (juveniles), figs. 4-8 (late morphotype) [not fig. 9 =early morphotype of *A. alata*]; NORRIS AND UYENO, 1981, Pl. 9, figs. 1-5, 8, 9, 16-21 (early morphotype), 28-29 (late morphotype); MOURAVIEFF, 1982, Pl. 2, fig. 4 (early morphotype); BULTYNCK, 1982b, p. 38, Pl. 1, figs. 26, 27 (early morphotype), Pl. 2, fig. 1 (early morphotype), 2 (late morphotype) [not fig. 3 =*A. alata* s.l.]; HOU, JI, WANG, WANG, AND ZANG, 1986, Pl. 3, figs. 9a, b (late morphotype); HOU, JI, XIAN, AND WANG, 1986, p. 123, Pl. 2, figs. 1-4, 7, 8 (late morphotypes).

Ancyrodella rotundiloba (Bryant). KLAPPER, 1985, p. 24-27, Pl. 1 figs. 1-20 (early morphotype), Pl. 2, figs. 1-4 (late morphotype), 5-12 (early morphotype); Pl. 3, fig. 1-4, 12 (late morphotype); 5-11 (early morphotype); Pl. 4, figs. 9-12 (late morphotype), Pl. 8, figs. 9, 10 (late morphotype), Pl. 11, figs. 3, 4 (late morphotype); GARCIA-LOPEZ, 1986b, Pl. 1, figs. 6, 7, 10(?), 11, 12 (late morphotype) [not Pl. 1, figs. 8-9 =*A. rugosa* Branson and Mehl, 1934]; ZIEGLER

AND WANG, 1986, Pl. 3, fig. 12 (early morphotype) [not figs. 7, 8]; GARCIA-LOPEZ, 1987, p. 64-66, Pl. 1, figs. 6, 7, 10(?) (late morphotype) [not figs. 8, 9 =*A. rugosa*]; SANDBERG ET AL., 1989, p. 212-213, Pl. 3, fig. 7 (the lectotype=late morphotype) [not figs. 1, 2, 5-6, 8-9 (=early morphotypes of *A. alata*), 3, 4 (=?*A. rugosa*)] [not Pl. 2, figs. 5, 6, 9, 10 (=early morphotypes of *A. alata*) and not Pl. 4, figs. 12, 13 (=morphotype of *A. alata*)].

Ancyrodella binodosa Uyeno. BULTYNCK AND JACOBS, 1981, p. 16, 17, Pl. 8, figs. 1-12 (alpha form=early morphotype of *A. rotundiloba*), 13, 14 (beta form=early morphotype of *A. rotundiloba*), Pl. 9, figs. 3-5, 7, 8 (delta form=form transitional between *A. binodosa* and early morphotype of *A. rotundiloba*), figs. 1, 2, 6 (gamma form=early morphotype of *A. rotundiloba*).

Polygnathus cristatus Hinde. HUDDLE, 1981, p. B28-29, Pl. 9, figs. 11-19, Pl. 10, figs. 7-17 (late morphotype of *A. rotundiloba* from Crosby Sandstone fide Klapper, 1985, p. 26).

Ancyrodella isabelae GARCIA-LOPEZ, 1986b, p. 448-449, Pl. 1, figs. 13-14, 15-16 (the holotype=early morphotype of *A. rotundiloba*); GARCIA-LOPEZ, 1987, p. 61-62, Pl. 1, figs. 11-12 (the holotype).

Ancyrodella soluta SANDBERG, ZIEGLER, AND BULTYNCK, 1989, p. 211-212, Pl. 1, figs. 5, 6, 11, 12 (=early morphotype of *A. rotundiloba*), Pl. 2, figs. 1, 2 (=late morphotype of *A. rotundiloba*), 3-4 (=early morphotype of *A. rotundiloba*).

Description.—The specimens from the lower Penn Yan Shale are highly variable in platform outline, in shape and size of the pit, and in the development of incipient keels. In these features, they are within the range of variability of *Ancyrodella rotundiloba* (Bryant), and all are the early morphotype of the species. In outline, the platform is typically heart-shaped, with rounded, rather weakly defined anterior lobes. The size and style of preservation of the specimens from the basal Penn Yan Shale (Black shale A) suggest the remains of an adult stage of a single species.

The pit is moderate in size and bilobate, with an asymmetrical (Plate 1, figures B-D, F) to diamond-shaped (Plate 1, figures A, I) outline. Some specimens have laterally or anteriorly directed incipient keels or swellings on one or both sides of the pit. In some specimens, the proximal ends of these keels or keel-like structures arise as bifurcations of the margin of the pit, and the distal ends are sometimes swollen. Especially distinctive is a fold in the platform on the inner side where the free blade joins the platform (Plate 1, figures F, I).

In the one specimen from Black shale A in which the upper surface is partially seen, the nodes are numerous (Plate 1, figure G), but the pattern of the nodes cannot be determined. In specimens from Black shale B, the upper surfaces display a symmetrical pattern in which a row of nodes on either side of the blade converges to the carina and parallels the carina to the posterior end (Plate 2, figure H). This symmetrical pattern is seen in the early morphotype in the North Evans Limestone (Plate 2, figure P), and higher in the Penn Yan Shale (Plate 2, figures K, N). The symmetrical pattern of nodes is also seen in late morphotypes of *A. rotundiloba* from the upper Penn Yan Shale (Plate 2, figures M, R) and in the lectotype of the species from the North Evans Limestone (Huddle, 1981, Pl. 1, fig. 1).

POLYGNATHUS CRISTATUS? Hinde, 1879

Plate 3, figures D, E, I, J

Polygnathus cristatus? Hinde. KLAPPER, 1989, p. 458, Pl. 3, fig. 14.

Remarks.—Klapper (1985, personal commun.; 1989) recognized this platform element to be morphologically and stratigraphically intermediate between those of *Polygnathus cristatus* Hinde (sensu Ziegler and Klapper, 1982a) and *Mesotaxis asymmetrica* (Bischoff and Ziegler). The diagnostic feature is the development of transverse ridges

on the anterior area of the upper surface of the platform. The outline of the platform is similar to that in *P. cristatus* and *M. asymmetrica*, but the nodes on the upper surface are coarser and fewer in number than in *M. asymmetrica*, and not aligned in parallel rows as in *P. cristatus*.

In the Montagne Noire, *Polygnathus cristatus*? Hinde ranges from the *disparilis* Zone into the lower part of the Lower *asymmetrica* Zone (Klapper, 1985, figs. 1, 2), equivalent to Zone 1 of Klapper (1989). In west-central and western New York, *P. cristatus*? Hinde occurs in the Lodi Limestone, which is correlated with the *norrisi* Zone.

Acknowledgments

I thank the following for help on this project: G. Baird and C. Brett for providing the majority of the samples, and for guiding me in the field and sharing their ideas about Genesee stratigraphy; G. Klapper for discussions on conodont taxonomy; my former students M. Huggins, C. Bresette, and V. Marks for work on the Lodi Limestone samples; J. Kralick for work on the SB shale horizon; N. O'Brien for assistance in the SEM work; R. Bitely for photographing the text figures; and J. Thompson and F. Collier of the National Museum of Natural History for making Bryant's types available for study. Grants from Potsdam College and the Research Foundation of the State University of New York supported the research. G. Klapper and T.T. Uyeno reviewed the manuscript.

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Appendix

Localities

Localities are listed from west to east (Figures 1, 3). Letter and number combinations refer to localities of deWitt and Colton (1978). Additional locality details are given in Kirchgasser et al. (1986), Baird et al. (1989), and Kirchgasser et al. (1989). Four-digit numbers are sample numbers. Abbreviation “M.N.” refers to Montagne Noire Zone of Klapper (1989) and Klapper and Johnson (1990).

- 1 **Taunton Gully (CI-2)** (Leicester 7 1/2-minute Quadrangle)—Section downstream of Starr Road bridge and falls over Genundewa Limestone, 2.7 km north of Leicester, Livingston County (Genesee Valley). Horizon 4583-SD of deWitt and Colton (1978, Plate 6) and Huddle (1981, p. B53). Western nodule bed of the Lodi Limestone with gastropods and leiorhynchid brachiopods is 15 cm thick and is capped by an 8 cm-thick black shale (?Black shale A). The Lodi horizon is 9.6 m above the base of the Genesee Formation and 0.84 m above the contact between the Penn Yan Shale and underlying Genesee Shale, which is at the top of the 0.25 m-thick black shale near the base of the falls.

3969—Lodi Limestone (*norrissi* Zone): *Skeletognathus norrisi* (2), *Polygnathus pennatus* (13), *P. cristatus*? Hinde sensu Klapper (1989) (6), *P. dengleri* (1).

- 2 **Beards Creek (CI-3)** (Leicester 7 1/2-minute Quadrangle)—Exposure in north and south embankments of Beards Creek downstream of falls over Genundewa Limestone, 0.48 km northwest of Leicester, Livingston County (Genesee Valley). Western nodule bed of Lodi Limestone is 21 cm thick and underlies an 8 cm-thick black shale (?Black shale A). The Lodi horizon is 10.0 m above the base of the Genesee Formation and 1.0 m above the contact between the Genesee and Penn Yan Shales, which is at the top of a 0.30 m-thick black shale.

3999—Lodi Limestone (*norrissi* Zone): *Skeletognathus norrisi* (2), *Polygnathus pennatus* (9), *P. dengleri* (8).

- 3 **Fall Brook (CI-4)** (Genesee 7 1/2-minute Quadrangle)—Section in tributary of Fall Brook at east end of the steep north embankment downstream of the main falls over the Genundewa Limestone, 2.4 km south of Genesee, Livingston County (Genesee Valley). Western nodule bed of the Lodi Limestone with gastropods and leiorhynchid brachiopods is 7.0 cm thick and underlies an 8.0 cm-thick black shale (?Black shale A). The Lodi horizon is 9.8 m above the base of the Genesee Formation and 0.81 m above the contact between the Genesee and Penn Yan Shales, which is at the top of the 0.23 m-thick black shale near the top of the first falls in the tributary. Horizon 19/4 of Kirchgasser (1981, p. 37, fig. 1).

3971, 3971a—Lodi Limestone (*norrissi* Zone): *Skeletognathus norrisi* (2), *Polygnathus pennatus* (16), *P. cristatus*? Hinde sensu Klapper (1989) (9), *P. dengleri* (6), *Icriodus symmetricus* (1).

- 4B **West Honeoye Valley** (Honeoye 7 1/2-minute Quadrangle)—Section in third tributary to Honeoye Creek south of Richmond Center, which crosses South Road 1.6 km north of Rte. 20A, 2.1 km northwest of Honeoye, Ontario County (Honeoye Valley). Section in lower Penn Yan Shale is about 200 m west of South Road. Pyritic discontinuity horizon at top of Black shale A of lower Penn Yan Shale at the contact with overlying grey turbiditic shales. Sampled horizon is 38 cm above the top of the Lodi Limestone (Bed B) and 0.91 m below the pyritic discontinuity horizon at the contact between the grey turbiditic shales and Black shale B (Figure 4).

3977—Top of Black shale A of lower Penn Yan Shale (M.N. Zone 1; Lower *asymmetrica* Zone): *Ancyrodella rotundiloba* (early morphotype) (3), *P. ordinatus* (1), *P. pennatus* (1), *Palmatolepis disparalvea* (1).

- 5A **Abbey Gulf (HY-5)** (Honeoye 7 1/2-minute Quadrangle)—Exposures in gully of west-flowing tributary to Honeoye Creek, 0.2 km east of Allens Hill Road, 2.6 km northeast of Honeoye, Ontario County (Honeoye Valley). Pyritic discontinuity horizon of the lower Penn Yan Shale at the contact with the underlying interval of grey mudstones. Sampled horizon is 2.0 m above the contact between the Genesee and Penn Yan Shales. Bed B of the Lodi Limestone crops out in the side creek at the Genesee–Penn Yan contact, but is missing in the section in the main gully. (Section in fig. 7A of Baird et al., 1989.)

3956, 3960, 3993, 4024—Base of Black shale B of lower Penn Yan Shale (M.N. Zone 1; Lower *asymmetrica* Zone). *Ancyrodella rotundiloba* (early morphotype) (5), *Polygnathus pennatus* (2), *P. pen-*

natus-caelatus intermediate (1), ammonoid *Ponticeras perlatum* (1).

5B Gully north of Abbey Gulf (HY-6) (Honeoye 7 1/2-minute Quadrangle)—Exposures in gully and waterfalls of unnamed west-flowing tributary of Honeoye Creek, 0.5 km north of Abbey Gulf (Loc. 5A). Section is about 300 m east of Allens Hill Road. Bed B of Lodi Limestone and Black shales A and B of lower Penn Yan Shale.

3988—Discontinuity horizon at top of Lodi Limestone (Bed B) exposed in side creek (?*norrisi* Zone): *Polygnathus dubius* (49), *P. dengleri* (2), *Icriodus symmetricus* s.l. (1).

4006—Discontinuity horizons with ostracodes and large styliolines in middle of 30 cm-thick Black shale A of lower Penn Yan Shale (?M.N. Zone 1; ?Lower *asymmetrica* Zone): *Skeletognathus norrisi*? (1), *Polygnathus dubius* (3), *P. dengleri*? (1).

4007—Discontinuity horizon at top of Black shale A with clumps of pyrite, fishbone debris, large styliolines; bedding-plane surfaces with *Leiorhynchus* shell hash occur a few centimeters below the top of Black shale A. (M.N. Zone 1; Lower *asymmetrica* Zone): *Ancyrodella rotundiloba* (early morphotype) (5), *Polygnathus dubius* (2), *Mesotaxis asymmetrica*? (1), *Polygnathus? caelatus*? (1).

4010—Discontinuity horizon at base of Black shale B at top of 1.5 m interval of turbiditic shale and mudstone; no conodonts.

6 Abbey Road (Bristol Center 7 1/2-minute Quadrangle)—Upper reaches (around 1,000 ft. elevation) of tributary to Honeoye Creek that crosses Abbey Road, 0.5 km north of intersection of Abbey Road and Bell Road, and 4.3 km northeast of Abbey Gulf (Loc. 5A), Ontario County (Honeoye Valley). Bed B of Lodi Limestone and Black shales A and B of Penn Yan Shale.

4003—Bed B of Lodi Limestone; no zonable conodonts.

3997, 4002—Discontinuity horizons within Black shale A (60 cm thick) of lower Penn Yan Shale, 13.0 cm above the top of Bed B of the Lodi Limestone, which consist of cross-laminated siltstone and fine carbonate debris interbedded with black shale; bedding-plane surfaces with large current-oriented styliolines and abundant ramiform elements of *Polygnathus dubius*. No zonally diagnostic conodonts.

7 Flatiron Road (Bristol Center 7 1/2-minute Quadrangle)—Exposures in tributary to Mud Creek adjacent to Flatiron Road below Andrews Cemetery, 1.3 km northeast of Bristol, Ontario County (Bristol Valley). Black shale A at the base of the Penn Yan Shale is a 2 mm-thick discontinuity horizon of pyrite, fishbones and teeth, quartz sand, and conodont elements at the contact of the Genesee and Penn Yan Shales. The interval of grey shale above Black shale A is about 1.5 m thick. The rusty seam at the contact between the grey shale and overlying black shales, siltstones, and silty shales may correlate with the base of Black shale B in the Honeoye Valley (Figure 4).

3996—Black shale A at contact of Genesee and Penn Yan Shales. (M.N. Zone 1; Lower *asymmetrica* Zone): *Ancyrodella rotundiloba* (early morphotype) (3), *Polygnathus pennatus* (2), *P. cristatus*? Hinde sensu Klapper, 1989) (1), *P.? caelatus* (1).

8A Vincent (Cd-6) (Bristol Center 7 1/2-minute Quadrangle)—Exposures in tributary to Mud Creek crossing Rte. 20A, 0.7 km north of Vincent, Ontario County. Section is 0.7 km northeast of village of Vincent. Black shale A is a 20 cm-thick band at the base

of the Penn Yan Shale, immediately overlying the top of the Genesee Shale. The base of Black shale B of the lower Penn Yan Shale is a pyritic seam at the contact between the 1.5 m-thick interval of grey shale and the overlying succession of black shales and siltstones.

4012—Base of Black shale A at contact between Genesee and Penn Yan Shales; 2 cm-thick interval of cross-laminated, calcareous siltstone and black shale with clumps of reworked pyrite (M.N. Zone 1; Lower *asymmetrica* Zone): *Ancyrodella rotundiloba* (early morphotype) (1).

3994—Rusty surface at top of Black shale A (M.N. Zone 1; Lower *asymmetrica* Zone): *Ancyrodella rotundiloba* (early morphotype) (7), *Polygnathus pennatus* (2), *P. collieri*? Huddle (1).

9 Bristol Harbor (Middlesex 7 1/2-minute Quadrangle)—Exposure at base of bluff on west side of Canandaigua Lake at the marina at Bristol Harbor condominiums, about 100 m north of Seneca Point, Ontario County. Black shale A of lower Penn Yan Shale is the 30 cm-thick band exposed near lake level and above a unit with septarian concretions at the top of the Genesee Shale. The 1.8 m-thick interval of interbedded thin siltstones and silty shales above Black shale A is believed to be equivalent to the interval of grey shale and turbiditic mudstone between Black shales A and B in the Bristol and Honeoye Valleys.

3995, 4011—Base of Black shale A at base of Penn Yan Shale; bedding-plane of pyrite, bone-bed debris and conodont elements at contact between Genesee and Penn Yan Shales; horizon f in section of fig. 7B of Baird et al. (1989) (M.N. Zone 1; Lower *asymmetrica* Zone): *Ancyrodella rotundiloba* (early morphotypes) (2), *Polygnathus pennatus* (1), *Palmatolepis disparalvea*? (1), *P.? caelatus*? (1).

17 Mill Creek (Lodi Glen) (Ov-10) (Lodi 7 1/2-minute Quadrangle)—Exposure in cliff adjacent to Silver Thread Falls in Mill Creek, 1.8 km upstream from Lodi Point Road, 3 km west of Lodi, Seneca County. Exposure illustrated by deWitt and Colton (1978, Pl. 3; Kirchgasser, 1981, p. 45, fig. 1). Type section of Lodi Limestone.

3979—Bed A of Lodi Limestone at contact between Genesee Shale and Penn Yan Shale (Sherburne Siltstone); 1 to 8 cm-thick articulate brachiopod shell hash and dactyloconarid calcarenite with styliolines and annulated forms (nowakiids?) (*norrisi* Zone): *Skeletognathus norrisi* (4), *Polygnathus pennatus* (26), *P. cristatus*? Hinde sensu Klapper, 1989 (2), *P.? caelatus* (2), *P. dengleri* (3), *Mesotaxis asymmetrica*? (3), *Palmatolepis disparalvea* (2), *Icriodus symmetricus* s.l. (60).

3013, 3013A, 3949—Bed B of Lodi Limestone; 23 cm-thick concretionary bed, 1.2 m above contact between Genesee Shale and Penn Yan Shale (Sherburne Siltstone); type horizon of ammonoid *Ponticeras perlatum* (Hall) (*norrisi* Zone): *Skeletognathus norrisi* (1), *Polygnathus pennatus* (25), *P. cristatus*? Hinde sensu Klapper, 1989 (2), *P. dengleri* (4), *Icriodus symmetricus* s.l. (2).

22 Hubbard Quarry (Gen-2) (Sheldrake 7 1/2-minute Quadrangle)—Shale pit on the east side of Rte. 89, 0.2 km south of the Ovid–Romulus town line, Seneca County. Bed B of Lodi Limestone and pyrite horizon of Fir Tree Limestone.

3962—Pyrite horizon of Fir Tree Limestone, upper Genesee Shale,

3.7 m below base of Lodi Limestone at the contact between Geneseo Shale and Sherburne Siltstone (?Upper *disparilis* Subzone): *Polygnathus dubius* (24), *P. dengleri?* (1), *P.? caelatus* (2), *Schmidtognathus?* sp. (2), *Icriodus symmetricus* s.l. (2).

- 31 **Venice Center** (Genoa 7 1/2-minute Quadrangle)—Exposures near mouth of south fork of unnamed west-flowing tributary of Big Salmon Creek, 0.9 km north of Long Hill Road and 0.8 km east of New York Rte. 34, 1.1 km northeast of Venice Center, Cayuga County.

3989—Lenses of detrital pyrite at top of Fir Tree Limestone of upper Geneseo Shale; horizon d in section of fig. 4E in Baird et al. (1989) (?Upper *disparilis* Subzone): *Polygnathus dubius* (15), *P. ordinatus* (6), *P.? caelatus* (9), *P. linguiformis?* (1), *Pandorinellina?* sp. (1), *Icriodus symmetricus* s.l. (17).

- 32 **Genoa** (Genoa 7 1/2-minute Quadrangle)—Exposures on northern of two closely spaced west-flowing tributaries of Big Salmon Creek, 1.1 km south of Rte. 90 and 0.5 km southwest of BM 976 and Rte. 34 in the village of Genoa, Cayuga County.

3978—Lenses of detrital pyrite at top of Fir Tree Limestone of upper Geneseo Shale; horizon d in section of fig. 4F in Baird et al. (1989) (?Upper *disparilis* Subzone): *Polygnathus dubius* (7), *P. ordinatus* (8), *P.? caelatus* (2), *Palmatolepis disparilis* group? (1), *Icriodus symmetricus* s.l. (10).

Possible mastodon gastrointestinal and fecal contents from the late Pleistocene of the Hiscock Site, western New York State

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Abstract

Abundant short conifer twig fragments occur in a late Pleistocene layer at the Hiscock Site, western New York State. Several of these have been identified as spruce (*Picea*) or tamarack (*Larix*). Mastodon bones are the most common animal fossil remains in this deposit. Several lines of evidence (physical condition, statistical comparison with digestive products of large herbivorous mammals, and similarity to mastodon-associated material reported in the literature) strongly suggest that these twigs represent mastodon gastrointestinal and fecal contents and thus provide some information on the diet, feeding methods, and habitat of these animals. Assuming this interpretation is correct, the available evidence is insufficient to determine whether the twigs reflect (A) a normal year-round diet, presumably lacking the more digestible foods and those not readily fossilized; (B) a winter diet; (C) a local diet; or (D) a starvation diet. Proper determination of the nature and variety of mastodon diet requires examination of identifiable digestive products associated with individual skeletons found throughout the species' range, combined with determination of the season of death by use of techniques such as analysis of tusk growth-increments.

Introduction

The habitat and diet of the North American late Pleistocene

mastodon, *Mammuth americanum*, has been a matter of debate for some time. It is commonly believed that these animals favored wooded environments and were primarily browsers, whereas the coeval mammoths (*Mammuthus* spp.) thrived in more open grasslands and were grazers (Hatt, 1965, p. 20, 21; Kurtén and Anderson, 1980, p. 344, 345; McAndrews and Jackson, 1988, p. 168, 169; Barnosky et al., 1988, p. 181, 182). Studies of the "stomach" contents of mammoths preserved in permafrost (Vereshchagin and Baryshnikov, 1982, p. 269; Sutcliffe, 1985, p. 115; Harington and Ashworth, 1986, p. 912, 915), as well as analysis of probable mammoth fecal boluses (Mead et al., 1986), provide some relatively firm insight into the ecology of these animals. Evidence of mastodon diets and habitats, however, is rather sketchy (McAndrews and Jackson, 1988, p. 169). Consequently, the discovery of possible *Mammuth* gastrointestinal and fecal contents at a fossiliferous late Quaternary site in western New York State is of interest.

Geological context

The Hiscock Site is a 0.8-hectare (1.9-acre) area located in the town of Byron, Genesee County, New York (U.S. Geological Survey, Byron, New York, 7 1/2-minute Quadrangle, 45° 05' 04"N, 78° 04' 57"W). The geomorphology, stratigraphy, paleontology, palynology, and chronology of this locality have been discussed in a number of recent reports (Laub, 1984, 1986, 1987, 1988; Steadman et al., 1986; Steadman and Miller, 1987; Muller and Calkin, 1988; Laub et al., 1988; Miller, 1988; Steadman, 1988; Fisher, 1988).

The "basement" of the Hiscock Site consists of an unfossiliferous layer of cobbles closely packed in a matrix of variably silty clay. The top surface of this layer forms a series of platforms and depressions (Laub et al., 1988, fig. 5). The depressions represent the basins of spring-fed pools (sensu King, 1988, p. 151, fig. 2). Partly filling these depressions is a complex unit of grey to brownish-grey gravelly clay that ranges in thickness from 0.0 cm to 90 cm. This unit is dominated by the bones of mastodon (*Mammuth americanum*) (at least 95% of those collected), with relatively sparse remains of caribou (*Rangifer tarandus*) and the California condor (*Gymnogyps californianus*). The spring deposit is suffused with short, slender twig fragments that are distributed virtually throughout its volume (Figures 1, 2). Their depositional origin is the focus of this report.

The age of the spring deposit is late Pleistocene, based upon radio-carbon dates on the twigs of 10,450±400, 10,930±90, and 11,250±140 years B.P. (Ives et al., 1964, p. 41; Laub et al., 1988, p. 69, Fig. 6, Tab.

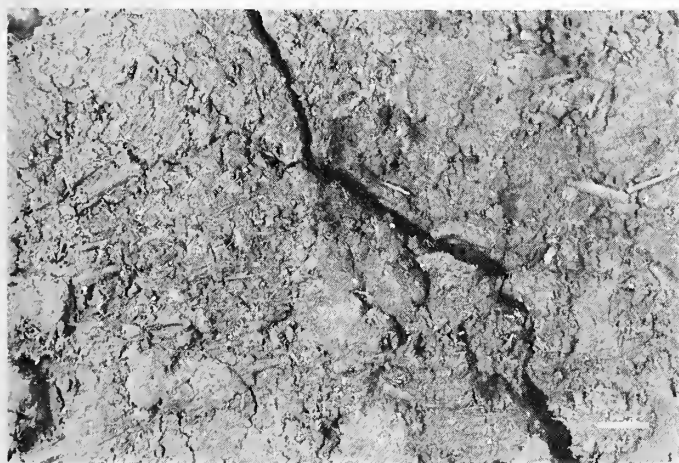


Figure 1. Sample of gravelly clay with twigs. White bar=1.0 cm.

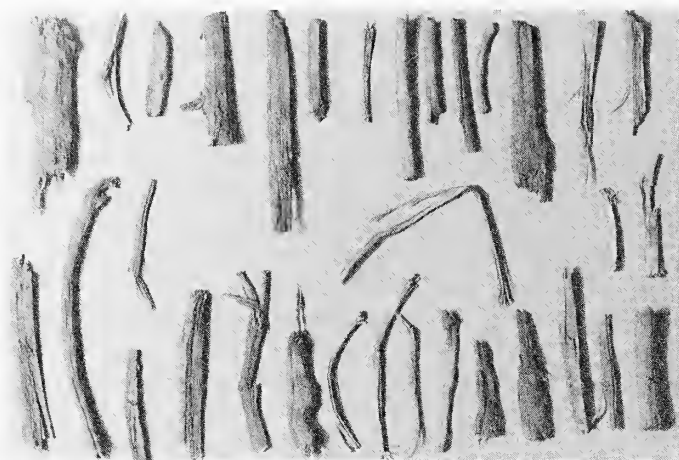


Figure 2. Examples of desiccated twig fragments from the Hiscock Site (H5NE-sample 2). These are among the larger and more robust twigs and are selected to illustrate their physical condition. Note variety of widths, generally truncated ends, and that the fragments commonly represent longitudinally split sections. White bar=1.0 cm.

1). Recently, a fragment of mastodon innominate bone was analyzed by use of the accelerator mass spectrometry technique (whole collagen) and yielded a date of $10,515 \pm 120$ years B.P. (Buffalo Museum of Science Hiscock Site specimen G5SE-138; Beta Analytic, Inc., lab no. Beta-24412; C^{13} adjusted).

Procedure

In an effort to determine the significance of the Pleistocene twig fragments, bulk samples (approximately $5 \times 15 \times 15$ cm) were cut from three locations in the undisturbed walls that were temporarily left to separate neighboring excavation pits (Figure 3). The blocks were sealed in plastic bags and refrigerated. In the laboratory, each sample was gently pulled apart by hand, and a subsample from the undisturbed center was carefully removed. These subsamples were disaggregated in a basin by the use of running water. All plant fragments 1.0 cm or greater in length were measured, and the results were plotted as histograms (Figure 4A-C). In addition, the physical condition of each twig was noted, particularly the appearance of the ends and evidence for splitting or crushing (Figure 2).

The reason for exclusion of particles under 1.0 cm in length is that the abundance and size of these smaller components made it impractical to measure them. In order to represent the contribution of these smallest fragments to the total volume of plant material, one of the Hiscock Site samples was selected for additional analysis. The contents of each size class were weighed and plotted to produce a histogram that shows an alternative size-frequency distribution (Figure 5A).

One possible explanation for the abundance of short, slender twigs is current sorting. These smaller fragments may have been transported downstream from a source area and separated from larger fragments. The flow regime at this site during the late Pleistocene cannot yet be determined, as only a small portion of it (less than 10%) has been excavated, and no obvious lateral gradient in twig size has been detected.

An alternative explanation involves deposition as fecal matter from living animals, and stomach and intestinal contents of dead ones. As nearly all of the bones found in this layer are of *Mammot americanum*, it is logical to hypothesize that if the plant material was deposited bio-

logically, this species was the agent. To test this idea, digestive products of large herbivorous mammals were sought for comparison.

One fecal bolus was obtained from each of two Asian elephants (*Elephas maximus*) at the Buffalo (New York) Zoological Gardens (Figure 6). The animal subjects were Lulu, a female about 38 years of age, and Surapa, a female about six years of age. The boluses, less than one day old and intact, were kept in separate plastic bags in a refrigerator. In the laboratory, each bolus was broken open gently by hand, and a subsample was removed from the core. No portion of the subsample had been exposed at the outer surface of the bolus. The components of the boluses, primarily timothy hay, had sufficient tensile strength that no significant breakage of the plant fragments should have occurred during laboratory separation. The subsamples were each disaggregated by soaking in tap water in a container (Figure 7). A sample of the hay

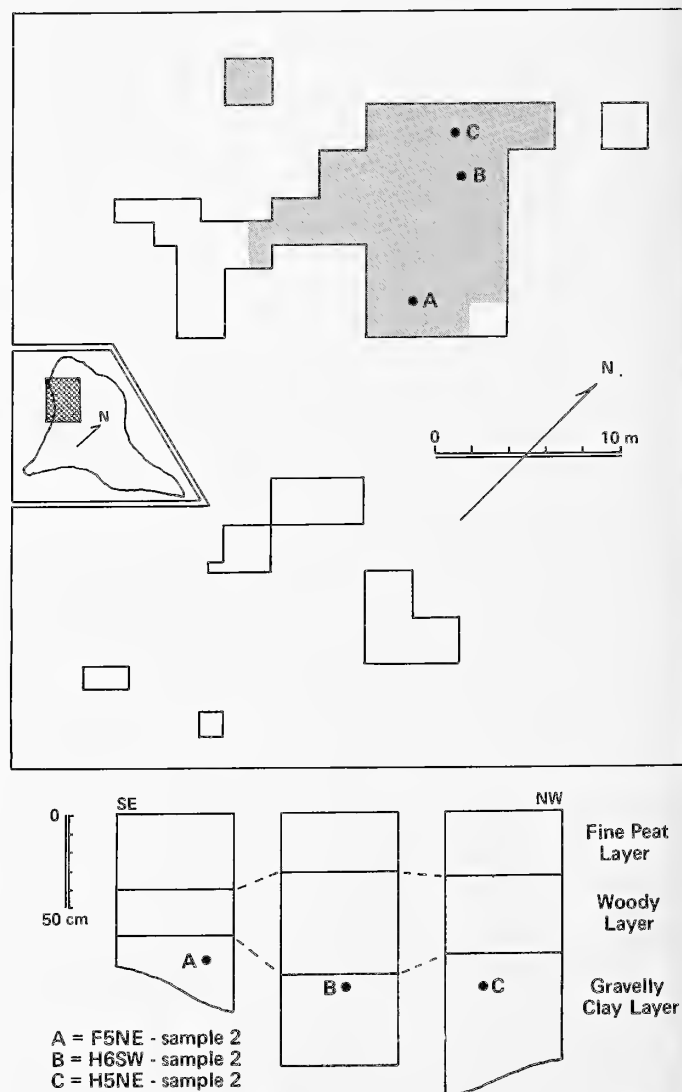


Figure 3. Excavated grid squares at the Hiscock Site, 1983 through 1988 field seasons, showing locations of the three samples of twig fragments used in this study. Areas where twig fragments occur in the gravelly clay layer are shaded. Stratigraphic context of each sample is shown at bottom of figure, and the location of the excavated area is overlain on an outline map of the entire site (as determined in 1986 by N.G. Miller and R.P. Futyma) in inset at left.

used to feed the elephants was examined for comparison with the bolus contents (see caption of Figure 9).

In addition, a box of twig fragments believed (on the basis of field context) to represent digestive products of very large ground sloths was loaned by G. Edmund (Department of Vertebrate Palaeontology, Royal Ontario Museum, Toronto) for analysis (Figure 8). These twigs represented bulk samples of plant material that were intimately associated with bones of *Eremotherium carolinense* (sensu Hoffstetter, 1952) in hydrocarbon-soaked fluviatile deposits at Talara, Piura Department, Peru. They have been dated at approximately 14,000 years B.P. (late Pleistocene; see Churcher, 1966, p. 992, 993). Although gomphothere remains occur at this site, the great majority of bones found there belong to ground sloths. The twigs were poured onto a sheet of paper, and the entire contents of a sector of the pile was taken as a subsample.

As with the Hiscock Site twig fragments, all plant fragments 1.0 cm in length or longer in the elephant and sloth subsamples were measured and assigned to size classes. The frequencies were plotted on histograms that show the percentage of total individual fragments within each class (Figure 4D-F). In addition, the contents of each class, including those in the range below 1.0 cm, were weighed and plotted on histograms (Figure 5B-D). The mean length and standard deviation of each of the six subsamples (three from the Hiscock Site, two elephant boluses, one assemblage of twigs from Talaxa, Peru) were calculated (Table 1 and Figure 9).

Results

The plots of relative frequency of twig lengths for all subsamples (Figure 4) approximate the right limb of a bell-shaped curve, with the frequency concentrated in the lower length classes and dropping off in the higher classes. In the case of the Hiscock subsamples, the frequency drops off rather abruptly above the 1.75 cm or 2.0 cm range, and almost no twigs longer than 4.0 cm are found. The mean lengths for all six of these relative frequency distributions fall within the rather narrow range of 3 mm (Table 1 and Figure 9). The standard deviations of the Hiscock Site twig fragments are greater than those of the sloth twigs and less than those of the elephant bolus contents.

Although these six histograms generally resemble each other, the total range of twig length is smallest for the sloth material. In the plot of weight distribution by size class (Figure 5), the relatively leptokurtic (high-peaked) nature of the sloth twig histogram, compared with those for the Hiscock Site material and the elephant boluses, is even more apparent. The amount of material by dry weight in the five classes

below 1.0 cm is by far the least for the Peruvian sloth subsample, and much greater for those of the elephants. The Hiscock Site subsamples fall slightly below the latter. This distribution parallels the order of the standard deviations in Table 1 and Figure 9.

It is unclear at this time whether the disparities between subsamples in the proportion of material in the smallest size classes (below 1.0 cm) reflect taphonomy or some aspect of the digestive process in the different kinds of animals involved. Structural strength of the plant material does appear to be a factor. The Peruvian sloth twigs include angiosperm wood (Rosaceae, according to R.H. Zander, personal commun., 1988). Informal tests that involved grinding twigs between two carpenter's files with a uniform number of strokes resulted in less shredding of the Peruvian material than occurred with the Hiscock Site fragments. The latter, in turn, shredded less than the timothy hay from the elephant boluses. Similar tests with wood from living spruce and hardwood trees and elephant hay-feed did not yield clear results.

Subsamples of the plant material from the Hiscock Site were examined by one of the authors (DJC) for the purpose of identifying some of the components. No obvious remains of grasses or leaves were found. The vegetation consists of conifer twig fragments, as far as has been determined. Some of the pieces retained their full circumference. Growth rings are present, and clearly indicate that the specimens are twigs rather than fractured sections of large branches or trunkwood. The rings demonstrate an individual age of about one to five years for the twigs. Commonly, the pieces were only a longitudinal portion of the twig from one-fifth to two-thirds of the original circumference. The ends were typically blunt rather than wedge-shaped, and this suggests that the force that led to breakage was directed perpendicular to the long axis (i.e., chopping), rather than along it (tearing or bending).

Ten twig specimens from H5NE-sample 2 were examined in thin-section. Of necessity, these were among the larger pieces. In three of them, sufficient structural detail was present to reveal resin canals with thick-walled epithelium and an absence of spirals, which indicate that these are either spruce (*Picea*) or tamarack (*Larix*). The condition of the twig fragments did not allow more precise systematic determinations. Spruce pollen is present in this level (albeit in fairly low relative frequencies; Miller, 1988, Figure 2), whereas tamarack pollen was not recorded. It would not be valid to assume, however, that the twigs are therefore spruce. The dispersal potential for tamarack pollen is less than that for spruce (N.G. Miller, personal commun., 1988), and tamarack could have been present in this area. Furthermore, tamarack twigs could have been eaten by animals elsewhere, transported in their alimentary tracts, and deposited at the site as products of digestion without leaving a significant pollen record.

A subsample of F5NE-sample 2 was examined by P.D. Horne

SAMPLE	SAMPLE SIZE	SAMPLE MEAN (cm)	SAMPLE STANDARD DEVIATION
H6SW - sample 2	288	1.66	0.66
H5NE - sample 2	309	1.59	0.55
F5NE - sample 2	302	1.77	0.65
Peruvian sample	264	1.74	0.53
"Lulu"	283	1.89	0.87
"Surapa"	434	1.74	0.77

Table 1. Mean twig length and standard deviation for measured samples.

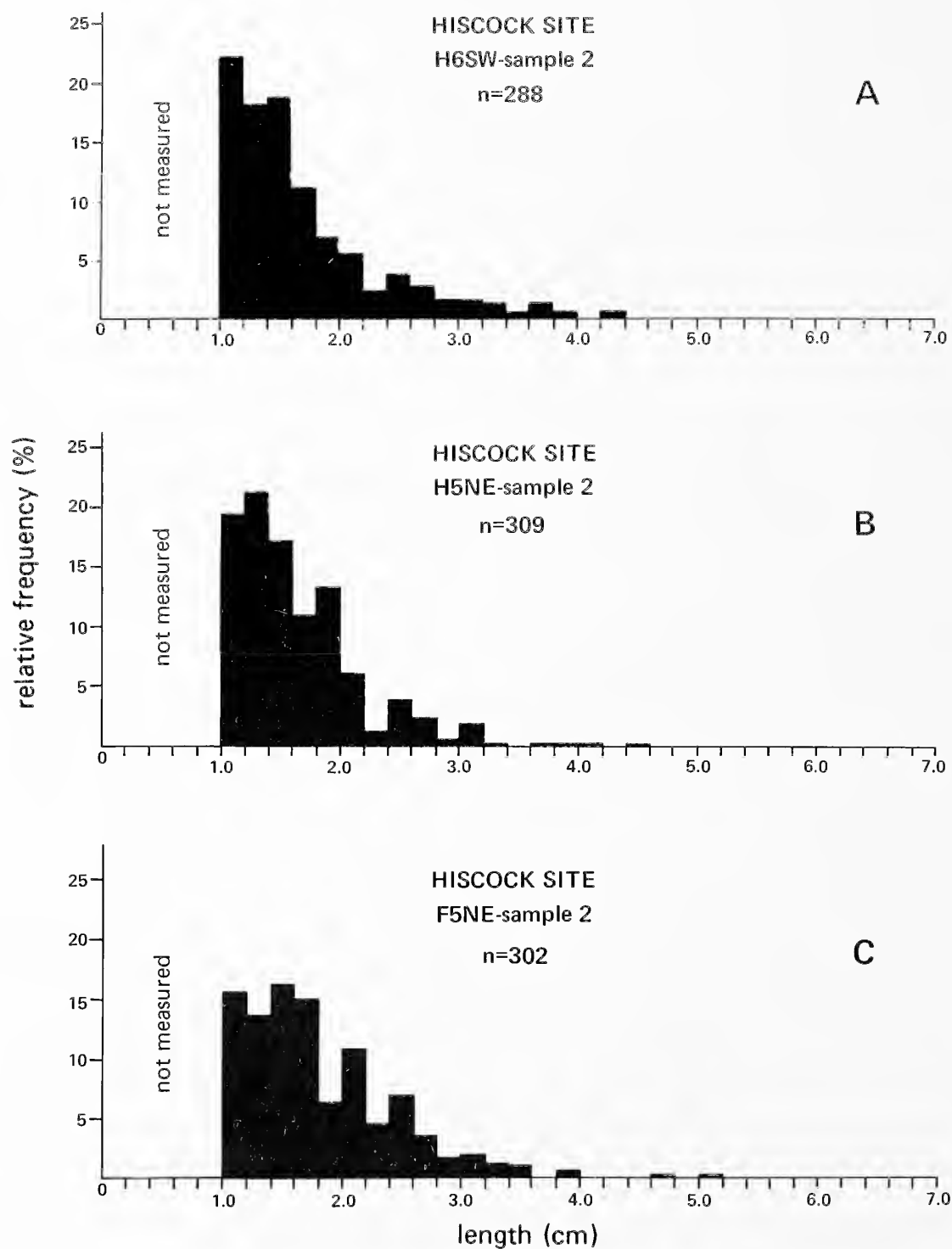
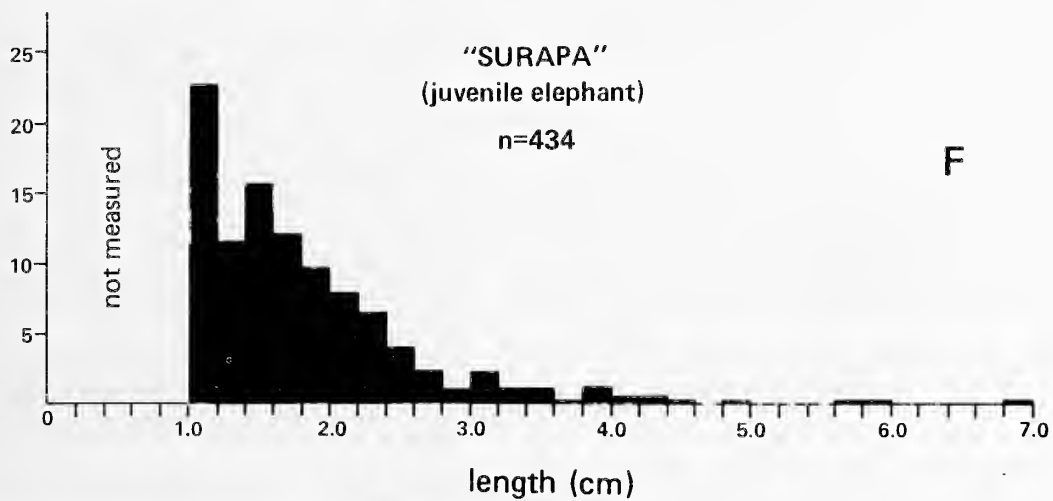
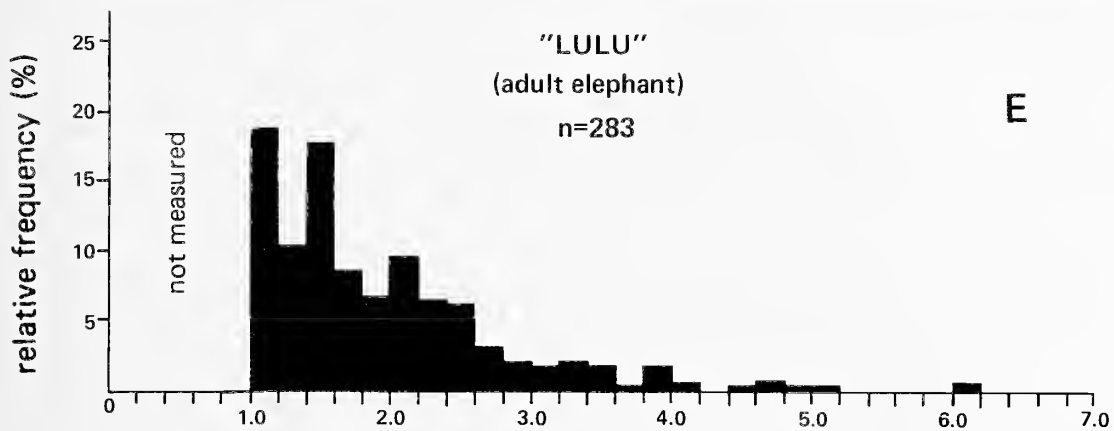
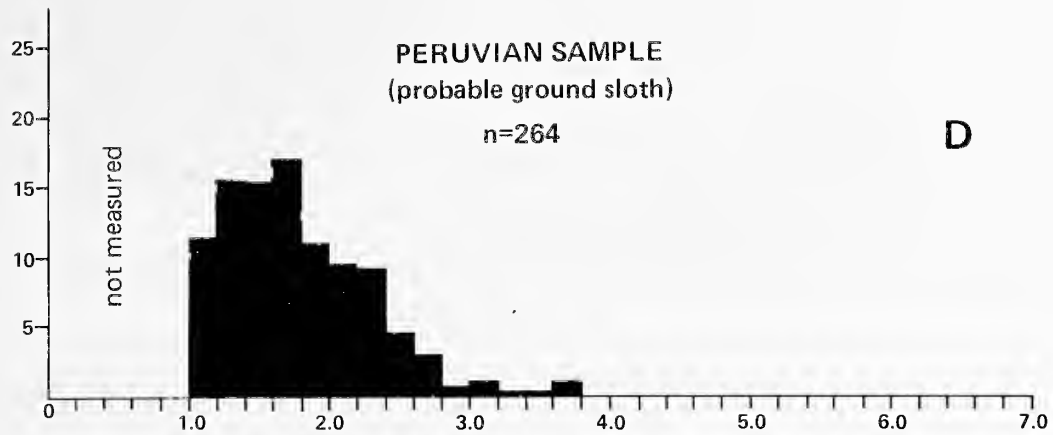


Figure 4. Relative length frequency distributions of twig fragments from the three Hiscock Site subsamples (A-C) compared with those for the Peruvian (D)



and elephant bolus (E, F) subsamples. Based on data in Table 2, standardized as percentage of total.

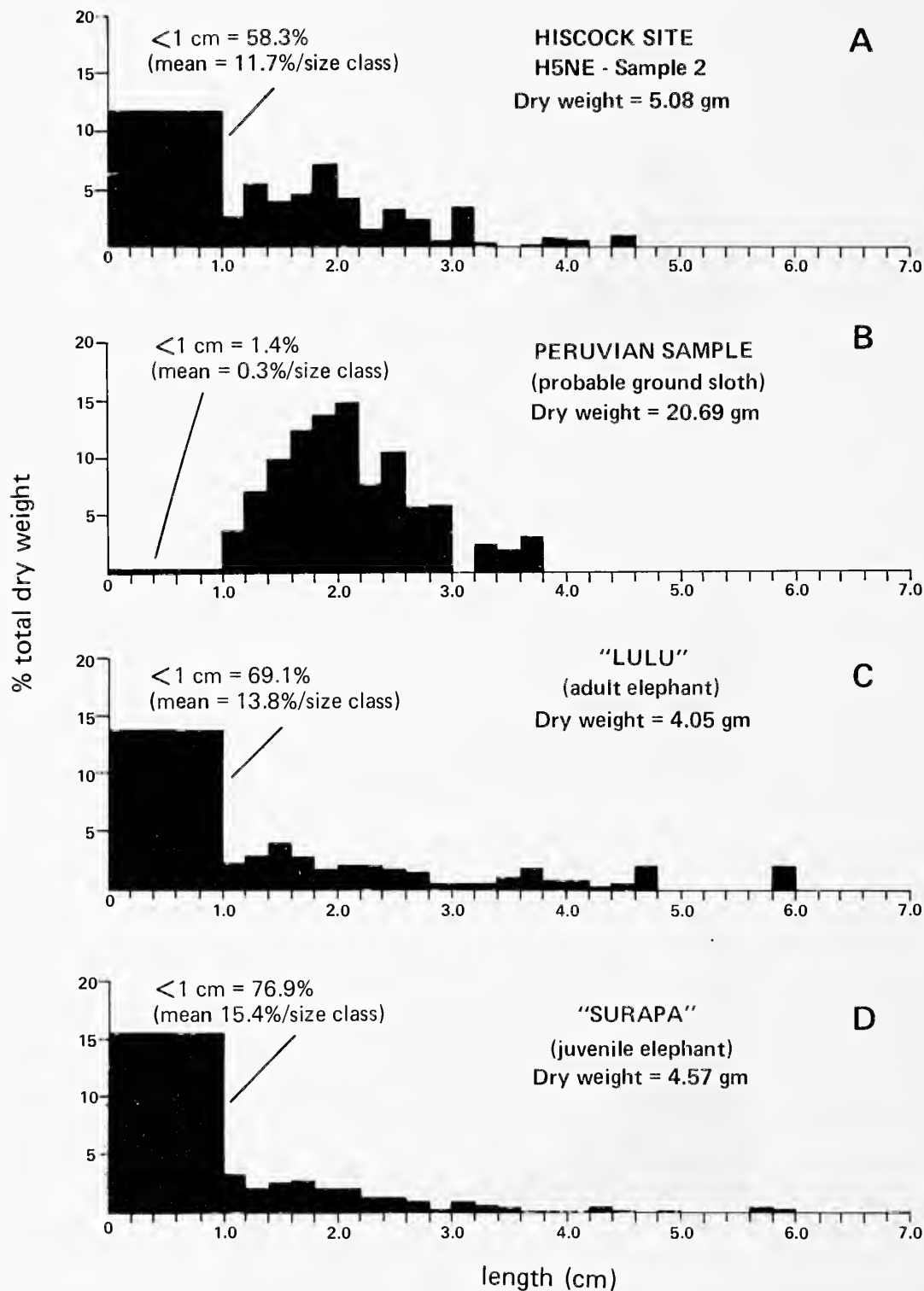


Figure 5. Relative length distribution by dry weight for one Hiscock Site twig subsample (A) and for the Peruvian (B) and elephant bolus (C, D) subsamples. Based on data in Table 3, standardized as percentage of total.



Figure 6. Fragment broken from elephant bolus to show internal features. White bar=1.0 cm.

(Pathology Laboratory, Women's College Hospital, Toronto) for parasite eggs that are sometimes present in animal digestive by-products. None were found in this material.

Similar material associated with other mastodon sites

Material comparable to that described herein has been reported in association with mastodon remains at a number of other sites, and has commonly been inferred to be "stomach contents." Dreimanis (1968, Tab. 2) provided an account of plant remains found in the rib cage area of mastodon skeletons. The following summary is drawn primarily from the sources he cited. It is not exhaustive, but it aims to show that concentrations of short vegetational fragments in conjunction with mastodon remains are not unique to the Hiscock Site.

Mitchill (1818, p. 376; fide Hartnagel and Bishop, 1922) noted mastodon remains excavated at Chester, near Goshen, New York, between 1807 and 1817. He had personally removed a number of bones from a layer of peat at this site. According to Hartnagel and Bishop

(1922, p. 46), "Beneath and immediately around the bones was a mass of coarse vegetable fibers said to resemble chopped straw—perhaps the remains of the last meal."

Maxwell (1844, p. 120) reported the discovery of five mastodon skeletons on Abraham Ayers' farm near Hackettstown, Warren County, New Jersey. Between the ribs of a number of the animals was found "a considerable quantity of what Mr. Ayers describes as resembling coarse chopped straw, mixed with fragments of sticks—no doubt the contents of the stomach." Charles Lyell (fide Hay, 1923, p. 67) referred to these skeletons and reported that between the ribs (presumably of one individual) were found seven bushels of plant material supposed to have been stomach contents. Lyell took some to London for microscopic examination, where it was identified as probably white cedar (*Thuja occidentalis*).

Asa Gray (1848, p. 92, 93) reported his examination of "earthy matter, filled with finely broken fragments of branches of trees," which was said to be from the stomach region of a mastodon skeleton unearthed at Schooley's Mountain, New Jersey. Hay (1923, p. 67) believed that this locality report was incorrect, and that the skeleton was one of those found near Hackettstown in the same county. Gray (1848, p. 92, 93) said that his sample "evidently consisted of branchlets of one, two and three years old, broken, quite uniformly, into bits of half an inch or so in length, with only, now and then, traces of the bark remaining on the wood. The wood was not at all fossilized, and was but slightly decayed." Microscopic examination of thin slices showed structure consistent with that of "common hemlock spruce" (probably eastern hemlock, *Tsuga canadensis*). There is some degree of similarity between cedar and hemlock wood (particularly at the macroscopic level), which may account for the difference between the identifications obtained by Lyell and Gray. This, of course, assumes that the samples did come from the same source.

Warren (1852, p. 144-148) discussed plant remains found with a skeleton (the "Warren Mastodon") near Newburgh, New York. About four to six bushels of this material was concentrated among the ribs, where it lay unmixed with other sediment. It extended for three feet in a four-inch-wide trail back under the pelvis "in the direction of the last of the intestines." Warren described it as consisting of twigs "broken into pieces of about two inches in length, and varying in size from very small twigs to half an inch in diameter." Much finer material that

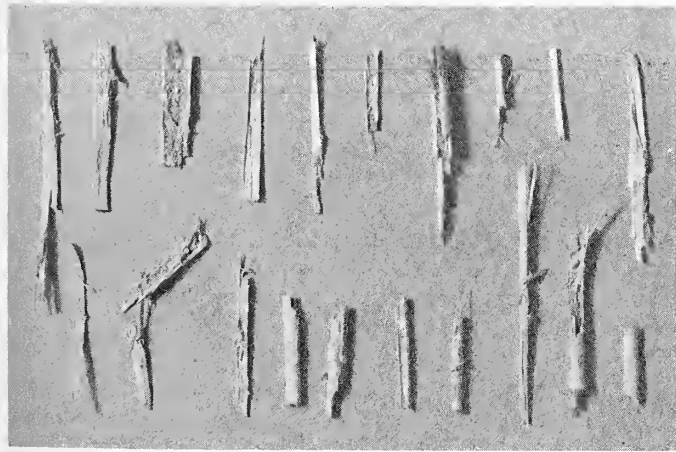


Figure 7. Examples of the larger (undesiccated) hay fragments removed from one of the elephant boluses ("Surapa") to show their physical condition. White bar=1.0 cm.



Figure 8. Examples of wood fragments from the Peruvian sample (associated with ground sloth bones) to show their physical condition. Note thorns in upper left. White bar=1.0 cm.

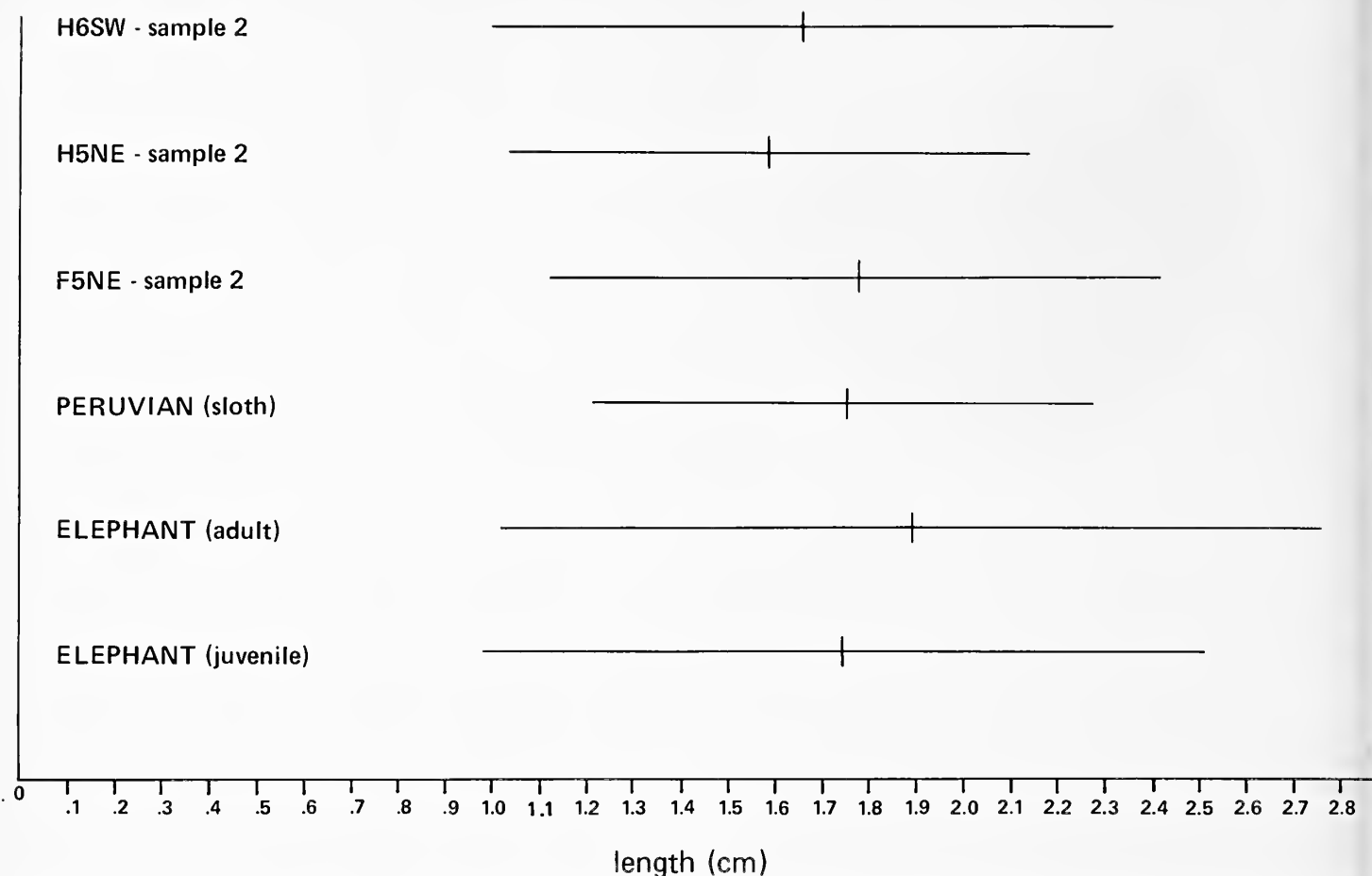


Figure 9. Mean of each of the six samples used in this study (short vertical bars). Long horizontal bars represent one standard deviation on either side of the mean. Based on data in Table 2. As a control for the measurements of the elephant bolus contents, the following statistics were determined for a sample (n=106) of the timothy hay used to feed the elephants: mean length=30.7 cm; range=6-94 cm; sample standard deviation=14.6 cm.

resembled torn leaves was present. At the time of excavation, this vegetational mass was considered to represent stomach contents. Microscopically, it appeared to include terminal branches of conifer trees, and Warren noted their similarity to remains found with the Chester Mastodon (Mitchill, 1818) and the "Cambridge" (probably Hackettstown, New Jersey) Mastodon. In 1989, one of the authors (RSL) found an uncatalogued sample of vegetation in the Vertebrate Paleontology Division of the American Museum of Natural History. According to the handwritten label, these were stomach or intestinal contents of the Warren Mastodon. The twig component of this sample closely resembled the material from the Hiscock Site.

Asa Gray identified the plant debris associated with the Warren Mastodon as "twigs of some coniferous tree or shrub, and probably some kind of spruce or fir" (quote from a letter to J.C. Warren, cited by Warren, 1852, p. 145). A Dr. Carpenter of London independently reported that a sample of this vegetation contained two kinds of wood fragments: very well-preserved reddish ones, probably conifer, and blacker, partly decomposed fragments. Warren (1852, p. 147) noted that no such material had been found in other bogs, and that it was not mixed with gravel or any other "foreign" substance. This information was given in support of the conclusion that the plant material represented the animal's processed food.

Cheney (1872, p. 178, 179) reported the remains of "*Mastodon giganteus*" near Jamestown, Chautauqua County, New York. Included in this report was a reference to discovering "in proximity to the viscer-

al cavity of the larger skeleton, a mass of undigested food, some eight or nine bushels in quantity, and consisting of slightly decayed twigs of two or three inches in length, identified as cone-bearing species, similar to our pines and firs, and remarkably preserved."

Stodder (1875, p. 91, 92) reported "contents of a mastodon's stomach" that had been collected at Wayland, New York. The plant material was examined by J.G. Hunt of Philadelphia, who identified abundant remains of "cryptogams" (spore-bearing plants), flowering species, moss "leaves" and stems (well-preserved), and one fragment of a water plant, possibly a rush, about an inch long. The absence of sphagnum and coniferous plant remains led Stodder to infer that "the pines and cedars, and their allies, formed no part of the mastodon's diet."

A mastodon found at Temple Hill, Orange County, New York (Bishop, 1921, p. 170; Hartnagel and Bishop, 1922, p. 52), had large masses of broken ("trituated," according to Bishop) "twigs and plant remains lying between the ribs." The remains came into view while the bones were being removed. Bishop described the plants as "apparently tamarack" and "evidently the creature's last meal."

Spillman (1929; *vide* Abel, 1935, p. 336) reported a complete mastodon skeleton, referred to *Bunolophodon postremus*, at Alangasi, Pichincha Province, Ecuador. As the skeleton was removed, there appeared a number of spherical objects, about 15 cm in diameter, in the pelvic region, in a position approximating that of the rectum. These were taken to represent fecal boluses. Their consistency was similar to that of horse dung. These aggregates of plant material were preserved in

SIZE CLASS (cm)	TRUE LIMITS (cm)	H6SW - SAMPLE 2	H5NE - SAMPLE 2	F5NE - SAMPLE 2	PERU SAMPLE	"LULU"	"SURAPA"
0 - 1.0	under 0.950	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.
1.0 - 1.2	0.950 - 1.149	64	60	47	30	53	99
1.2 - 1.4	1.150 - 1.349	52	66	41	41	29	50
1.4 - 1.6	1.350 - 1.549	54	53	49	40	50	68
1.6 - 1.8	1.550 - 1.749	32	34	45	45	24	52
1.8 - 2.0	1.750 - 1.949	20	41	19	29	19	42
2.0 - 2.2	1.950 - 2.149	16	19	33	25	27	34
2.2 - 2.4	2.150 - 2.349	7	4	14	24	18	27
2.4 - 2.6	2.350 - 2.549	11	12	21	12	17	17
2.6 - 2.8	2.550 - 2.749	8	7	11	8	9	9
2.8 - 3.0	2.750 - 2.949	5	2	5	2	6	4
3.0 - 3.2	2.950 - 3.149	5	6	6	3	5	9
3.2 - 3.4	3.150 - 3.349	4	1	4	1	6	4
3.4 - 3.6	3.350 - 3.549	2		3	1	5	4
3.6 - 3.8	3.550 - 3.749	4	1		3	1	1
3.8 - 4.0	3.750 - 3.949	2	1	2		5	5
4.0 - 4.2	3.950 - 4.149		1			2	2
4.2 - 4.4	4.150 - 4.349	2					2
4.4 - 4.6	4.350 - 4.549		1			1	1
4.6 - 4.8	4.550 - 4.749			1		2	
4.8 - 5.0	4.750 - 4.949					1	1
5.0 - 5.2	4.950 - 5.149			1		1	
5.2 - 5.4	5.150 - 5.349						
5.4 - 5.6	5.350 - 5.549						
5.6 - 5.8	5.550 - 5.749						1
5.8 - 6.0	5.750 - 5.949						1
6.0 - 6.2	5.950 - 6.149					2	
6.2 - 6.4	6.150 - 6.349						
6.4 - 6.6	6.350 - 6.549						
6.6 - 6.8	6.550 - 6.749						
6.8 - 7.0	6.750 - 6.949						1

n.m. = not measured

Table 2. Total number of twig fragments in each size class. n.m.=not measured.

glycerine, but Abel noted that no accurate study had yet been made of them. Unfortunately, no information was given about the physical nature of the boluses' contents.

Bryan et al. (1978) described the apparently butchered remains of a juvenile *Haplomastodon* found at Taima-taima, Venezuela. A concentration of small twig fragments, in fresh condition, was found closely associated with the bones. Six of these twigs, ranging in length from 2.0 to 4.2 cm, were shown in Figure 4 of their article and agree remarkably well with the material from the Hiscock Site. Bryan and his colleagues hypothesized that these twigs represented stomach or intestinal contents of the animal. They described them as "sheared" at both ends, "as if masticated," apparently meaning that the ends were broken straight across. These same twigs were illustrated by Sutcliffe (1985, p. 37, fig. 4.3).

Discussion

Not enough is known of the Hiscock Site's structure and sedimentology to allow current sorting to be rejected with confidence as the agency for accumulation of these twig fragments. However, two pieces

of evidence appear to weigh against this hypothesis: (1) The force that led to breakage appears to have been a chopping rather than a bending one, on the basis of the conditions of the twig ends. (2) Some of the twig fragments, while falling within the narrow range of length typical of associated material, display unusually great widths (e.g., Figure 2, top row, first and fourth twig from left; bottom row, first twig on right). This suggests that sorting has been more by length than by volume.

A credible alternative hypothesis for the origin of the twigs is that they were deposited as the gastrointestinal contents of dead mastodons, and as fecal bolus material of living ones. It is the preponderance of the bones of this species in the Pleistocene layer at the site that makes *Mammot americanum* the prime candidate. Although caribou (*Rangifer tarandus*) are represented here by rare fossils, they are not known to favor a diet of conifer vegetation, even when they dwell in spruce-tamarack forests. Also, the contents of their feces are much smaller than typical Hiscock twig fragments (A.E. Spiess, personal commun., 1991).

Three lines of evidence examined in this study appear consistent with the idea that the Pleistocene twig fragments at the Hiscock Site are products of digestion by mastodons:

1. *Statistical analysis.* Plots of the size frequency distribution based on individual twig fragments 1.0 cm or greater in length produce similar curves for the three Hiscock Site subsamples, the two elephant boluses, and the Peruvian material associated with ground sloth bones (Figure 4). The means of all six distributions are quite close, and fall within a range of 3.0 mm. In addition, the standard deviations of the Hiscock distributions are bracketed between those of the Peruvian twigs and the elephant bolus contents.

It is, of course, interesting to try to relate the mean twig length of the Hiscock fragments to some aspect of the masticatory apparatus of the mastodon, such as spacing of cross-lophs. One difficulty presented by the Hiscock assemblage is that a number of individuals of various ages are represented. A tusk count indicates the remains of a minimum of five mature and two immature mastodons in the roughly 8% of the areal extent of the site excavated as of 1990. The relationship between loph spacing and twig length would thus be confused by the mixing of digestive products of individuals with different-sized teeth. Another difficulty lies in our ignorance of how the mastodon chewed. Rather than converging anteriorly as in most animals, the maxillary dental bat-

teries of *Mammot americanum* diverge (e.g., Olsen, 1979, Fig. 2; Royal Ontario Museum mounted skeleton, ROM 65). This contrasts with the more conventional anterior convergence of the mandibular batteries. Thus it seems unlikely that mastication was a simple up-down motion, or a simple antero-posterior displacement as in the Elephantidae (Maglio, 1973, p. 101, Fig. 38; Eltringham, 1982, p. 228).

Of possible significance is the virtual absence of twig fragments greater than 4.0 cm in length. This approximates the cross-loph spacing in the largest teeth (M3) and might be anticipated as a significant upper size limit of masticated twigs, however the jaws were moved.

2. *Physical condition.* The Hiscock twigs are noteworthy for their common longitudinally split condition, the generally abrupt truncation of their ends, and the fact that the wood shows little modification (other than the loss of bark) from what must have been its original appearance. This agrees well with the condition of the elephant and supposed sloth material. The recognizability of plant material in elephant feces is well-known, and even such succulent feed as red beets may pass unaltered through the animal's digestive tract (Benedict, 1936, p. 189; Eltringham, 1982, p. 33). The apparently chopped

SIZE CLASS (cm)	TRUE LIMITS (cm)	H5NE- SAMPLE 2	PERU SAMPLE	"LULU"	"SURAPA"
0 - 1.0	under 0.950	2.96	0.29	2.80	3.51
1.0 - 1.2	0.950 - 1.149	0.13	0.75	0.09	0.15
1.2 - 1.4	1.150 - 1.349	0.28	1.45	0.11	0.09
1.4 - 1.6	1.350 - 1.549	0.20	2.03	0.16	0.12
1.6 - 1.8	1.550 - 1.749	0.23	2.53	0.11	0.13
1.8 - 2.0	1.750 - 1.949	0.37	2.78	0.07	0.09
2.0 - 2.2	1.950 - 2.149	0.21	3.05	0.08	0.09
2.2 - 2.4	2.150 - 2.349	0.07	1.60	0.08	0.06
2.4 - 2.6	2.350 - 2.549	0.16	2.18	0.07	0.06
2.6 - 2.8	2.550 - 2.749	0.12	1.20	0.06	0.04
2.8 - 3.0	2.750 - 2.949	0.03	1.21	0.02	0.01
3.0 - 3.2	2.950 - 3.149	0.17		0.02	0.04
3.2 - 3.4	3.150 - 3.349	0.02	0.48	0.02	0.03
3.4 - 3.6	3.350 - 3.549		0.40	0.04	0.02
3.6 - 3.8	3.550 - 3.749	0.01	0.74	0.07	0.01
3.8 - 4.0	3.750 - 3.949	0.04		0.03	0.01
4.0 - 4.2	3.950 - 4.149	0.03		0.03	0.01
4.2 - 4.4	4.150 - 4.349			0.01	0.02
4.4 - 4.6	4.350 - 4.549	0.05		0.02	0.01
4.6 - 4.8	4.550 - 4.749			0.08	
4.8 - 5.0	4.750 - 4.949				0.01
5.0 - 5.2	4.950 - 5.149			*	
5.2 - 5.4	5.150 - 5.349				
5.4 - 5.6	5.350 - 5.549				
5.6 - 5.8	5.550 - 5.749				0.02
5.8 - 6.0	5.750 - 5.949			0.08	0.01
6.0 - 6.2	5.950 - 6.149				
6.2 - 6.4	6.150 - 6.349				
6.4 - 6.6	6.350 - 6.549				
6.6 - 6.8	6.550 - 6.749				
6.8 - 7.0	6.750 - 6.949				0.05

* = one piece present, weight insufficient to record

Table 3. Total dry weight (gm) of twig fragments in each size class.

nature of the twig ends commonly observed in the Hiscock material would seem to suggest mastication of some sort rather than breakage by storms, water flow, or trampling in a sediment that probably had a high water content.

3. *Similar material at other mastodon sites.* A number of reports (cited above) note material similar to that of the Hiscock Site found in association with mastodon remains. Of the eight reports, two (Mitchill, 1818; Spillman, 1929) provide no identification of the plant material. Five (Maxwell, 1844; Warren, 1852; Cheney, 1872; Bishop, 1921; and Bryan et al., 1978) refer to short sections of twigs, and all but the last of these reports specify conifer twigs. Only one report (Stodder, 1875) specifically states that conifer material was not found. Reference to the plant material as having the appearance of "chopped straw" (Mitchill, 1818, fide Hartnagel and Bishop, 1922, p. 46; Maxwell, 1844, p. 120) calls to mind the impression that these vegetational concentrations gave when first encountered at the Hiscock Site.

The position of this fragmented plant material within the rib cage or visceral region of the skeletons (e.g., Warren, 1852; Cheney, 1872), and its occurrence in large aggregates (several bushels) relatively unmixed with surrounding sediment (Warren, 1852, p. 147), has commonly led its discoverers to view it as representing the animal's diet. This conclusion seems reasonable.

The reported twig fragment lengths are, in some cases, comparable to those of the Hiscock Site specimens (e.g., Gray (1848) on the New Jersey mastodon material; the twigs figured by Bryan et al. (1978) from Venezuela). In other cases, however, they are rather longer than those from the Hiscock Site (e.g., Warren (1852, p. 144) for the Warren Mastodon; Cheney (1872) for a mastodon found near Jamestown, New York).

The relatively unaltered condition of the plant material in these occurrences is commonly mentioned. Bryan et al. (1978) described the Venezuelan material as sheared at both ends, and Gray (1848) alluded to the virtual absence of bark from the New Jersey mastodon-associated samples.

In general, other published accounts of plant material associated with mastodon bones refer repeatedly to features similar to those of the Hiscock Site material, although details (such as size of twigs) may vary. The authors of this report feel that these recurrent references strongly support the interpretation that these various deposits of plant material originated through similar agencies that probably involved mastodon digestive activity. The absence of bark, however, ought not to have too much significance accorded to it. Conifer bark is quite thin toward the distal end of a branch. Although the living cells and photosynthetically produced nutrients concentrated in the inner bark might have been a source of nutrition for mastodons, this bark probably could also be removed through non-biological agencies and crumbled beyond recognition.

In summary, then, three lines of inquiry provide evidence consistent with the hypothesis that the twig fragments concentrated in the Pleistocene layer at the Hiscock Site are the digestive products of large herbivores. The preponderance of mastodon remains in this layer suggests *Mammot americanum* as the agent of accumulation and deposition.

A serious gap remains in the evidence for a gastrointestinal or fecal origin of the Hiscock twigs as presented here, especially in connection with the statistical analysis (above). This gap is the absence of a control sample taken from a population of twigs in a similar sedimentary setting known to have been concentrated through non-animal agencies. Location of an appropriate population, however, would seem to be a

study in itself, and this step regrettably will have to await future work in which the conclusions of this paper are tested.

Modern elephants eat great quantities of food, and there is always a large amount of fecal matter in the rectum or approaching it (Benedict, 1936, p. 184). The production and elimination of waste products by mastodons must have been great. Benedict (1936, p. 181) reported that a captive Asian elephant that was fed on hay produced 75 to 133 boluses per day. These observations, combined with the fact that modern elephants freely defecate in their water holes (C.S. Churcher, personal observation, personal commun., 1988), suggest that a major portion of the twig fragments in question are likely to be fecal in origin if they were processed by mastodons. Thus the twigs would represent the least digestible part of the diet. The proportion that represents gastrointestinal contents from carcasses (as distinct from feces from live animals) cannot be estimated until continued excavation provides a clearer idea of the minimum number of individuals preserved at the site.

If the conifer twig fragments are food remnants, then what type of diet do they represent? Was it a normal, year-round diet, a winter diet, a local diet, or perhaps a food of last resort during times of famine?

1. *Normal, year-round diet.* The samples from the Hiscock Site appear to consist entirely of conifer wood, and the narrow diameter and young age suggested by the growth rings indicate that the animals browsed the distal ends of branches. The guts of modern elephants contain protozoans and bacteria that produce cellulase, an enzyme that breaks down cellulose. The products of this reaction, along with the dead microfauna and microflora of the gut, provide nutrition to the animal (Eltringham, 1982, p. 89). Presumably, a similar process occurred in the mastodon. Can it be assumed, however, that the normal diet of this species was a unvarying one dominated by conifers, possibly of a single type? The available data do not justify such a conclusion. Only a small number of twigs have been examined in sufficient detail to allow taxonomic assignment below the level of "conifer." Further examination of the plant contents of the gravelly clay layer is planned over the next few years to increase the number of identified specimens for a more accurate picture of their taxonomic composition. As of the completion of this manuscript, preliminary studies suggest that the Hiscock Site twig fragments do include coniferous genera other than *Picea* and *Larix*.

Modern elephants have a diet that consists largely of grasses, but that also includes vines, trees, and shrubs (Benedict, 1936, p. 166, 171; Eltringham, 1982, p. 102, 103). Mammoths appear to have had a similar diet that emphasized grasses, but that included browsed woody material (e.g., Vereshschagin and Baryshnikov, 1982, p. 269; Sutcliffe, 1985, p. 115; Mead et al., 1986, p. 124). It is possible that mastodons had a similarly varied diet, with the remains found at the Hiscock Site representing only the least digestible components of that diet. Conifer needles, for example, were not recognized in the samples. If spruce is represented by the twig fragments (a proposition not yet demonstrated), then the animals must have been ingesting large amounts of needles along with the distal portions of branches. Were the needles completely digested, or simply not preserved? If tamarack is a major component of these twigs, the absence of their needles might be explained by feeding during the late fall and winter, when tamaracks lose their needles. At least one of the adult mastodons at the Hiscock Site, however, perished in mid-spring (Fisher, 1988, p. 121, 122), a time when tamarack needles should have been available if these trees were present. Feathers have been preserved in this layer (Steadman, 1988, p. 104), so the depositional environment should also have been conducive to the preservation of undigested conifer needles. Stomach contents of mastodons ought to approximate the natural diet of the animals more closely than would

intestinal or fecal material, because they would have been subjected to the digestive process for a shorter time. If such material can be recognized in association with a mastodon skeleton, some of the less-resistant foods may be identifiable.

2. *Winter diet.* It has been suggested that the mammoths' diet varied seasonally, with the animals concentrating on grasses and legumes during most of the year and browsing on trees and shrubs during the winter (Kurtén and Anderson, 1980, p. 354; Vereshschagin and Baryshnikov, 1982, p. 269; Sutcliffe, 1985, p. 115). If this was the case, it is possible that the mastodon similarly varied its diet opportunistically with the seasons. The preponderance of conifer remains at the Hiscock Site (so far as a limited examination of the twigs has revealed) might reflect a strong bias toward death of individuals during the winter, when conifer trees may have been the main source of food.
3. *Local diet.* In view of the extensive geographical range of *Mammuth americanum*—from Alaska to Florida, across the Great Plains, and its abundance in eastern North America (Kurtén and Anderson, 1980, p. 344)—it seems likely that this species was adapted to a variety of foods. Might the conifer diet suggested by the Hiscock Site remains, and by several earlier reports cited above, merely reflect the fact that they pertain to finds in the northeast, where spruce and tamarack were abundant?

Similarly, might the non-conifer material reported by Stodder (1875) to be associated with mastodon remains reflect a diet not limited by winter? Alternatively, might it reflect an environment other than a conifer forest?

4. *Starvation diet.* It is necessary, of course, to consider the possibility that the plant remains reflect material ingested by animals in time of famine. If so, then one would conclude that the other sites that preserve similar "stomach contents" all contain the remains of animals that died of starvation, rather than of some other cause. This hypothesis would be supported by demonstrating the existence of other kinds of gastrointestinal contents at a substantial number of mastodon sites in the northeast, which would mark animals that perished from causes other than starvation.

Conclusion

It appears probable that the short twig fragments that suffuse the late Pleistocene gravelly clay layer at the Hiscock Site represent digestive products (gastrointestinal and fecal) of mastodons (*Mammuth americanum*). If so, the animals were browsing the distal ends of conifer branches that belong to spruce (*Picea*) or tamarack (*Larix*) and possibly other types.

It has not been determined whether other more digestible or taphonomically less-preservable plant materials were a component of the diet of mastodons. In addition, the possibility that this diet typifies only certain seasons of the year or parts of the species' geographical range cannot be discounted on the basis of available evidence.

To determine the diet of *Mammuth americanum* more confidently, and to eliminate the biases of geography and season, it will be necessary to examine identifiable gastrointestinal material associated with individual skeletons that occur throughout the known range of the species. Material concentrated toward the front of the skeleton would more likely represent stomach (rather than intestine or caecum) contents, and might contain food in a less-digested state than that which was passing through the gut when the animal died. The season of the

individual's death (and thus the season reflected by the diet) could be determined by means of the tusk growth-increment technique of Fisher (1984, p. 353; 1988).

Acknowledgments

This study benefited greatly from the comments and assistance of a number of persons: C.S. Churcher (Zoology Department, University of Toronto); G. Edmund (Vertebrate Palaeontology Department, Royal Ontario Museum, Toronto); M.E. Georgi (Diagnostic Laboratory, New York State College of Veterinary Medicine, Cornell University); R.W. Graham (Illinois State Museum, Springfield); P.D. Horne (Pathology Laboratory, Women's College Hospital, Toronto); E. Landing (New York State Geological Survey); M.J. LoVullo, L. Vanderwalker, K. Chmelko, and R. Owlett (Buffalo Zoological Gardens, Buffalo, NY); J.I. Mead (Geology Department, Northern Arizona University, Flagstaff); N.G. Miller and D.W. Steadman (New York State Biological Survey); H.E. Savage (Anthropology Department, University of Toronto); A.E. Spiess (Maine Historic Preservation Commission, Augusta); D.B. White (Statistics Department, State University of New York, Buffalo); R.H. Zander (Botanical Division, Buffalo Museum of Science, Buffalo, NY); and D.F. Zinkel (Forest Products Laboratory, U.S. Department of Agriculture, Madison, WI). Technical assistance in producing the manuscript was given by M.C. Biber (data compilation), J.G. Manias (drafting), and V.E. Scimé (data compilation and typing). C.S. Churcher and R.W. Graham reviewed the manuscript. The Buffalo Museum of Science supplied \$150 toward publication of this report.

Excavation of the Hiscock Site was carried out through the courtesy of Doris W. Hiscock and the late Charles D. and Charlotte S. Hiscock. The project was funded principally through grants (to RSL) from the George G. and Elizabeth G. Smith Foundation of Buffalo, and with the support of the Buffalo Society of Natural Sciences. Valuable logistical assistance was given by the Herbert F. Darling Company (Engineering Contractors) of Williamsville, NY. Finally, we acknowledge with profound thanks the scores of volunteers without whose enthusiastic participation the past eight field seasons at the Hiscock Site would not have been possible.

Note added in proof

J.M. McAndrews (Royal Ontario Museum, Toronto) has found numerous spruce needle bases in a bulk sample from the Hiscock Site's Pleistocene horizon. In this report's analysis of the twigs, it was not possible to determine whether they were spruce or tamarack; and although pollen strongly suggested the presence of spruce, this report could not be more definite. McAndrews' find strengthens the probability that the twigs are spruce rather than tamarack—a conclusion with important implications, as no known animals feed on spruce.

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Redescription of *Styliolina* [INCERTAE SEDIS]— *Styliolina fissurella* (Hall) and the type species *S. nucleata* (Karpinsky)

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Abstract

Examination of topotypes of *Styliolina nucleata* (Karpinsky, 1884) from the Ural Mountains demonstrates that the species and the genus have been erroneously interpreted throughout the second half of this century. The type species *Styliolina nucleata* is redescribed, as is the genus. Restudy of the type collection of *Styliolina fissurella* (Hall, 1879) indicates that this species has been inadequately described, that several of the syntypes have been misidentified, and that the type collection has been erroneously assigned to formation and locality. *Styliolina fissurella* is redescribed and the topotype locality documented from the Ledyard Member of the Ludlowville Shale at Alden, New York.

Introduction

Styliolina is generally considered to be a small, smooth, thin-walled dactyloconarid with a worldwide distribution and an Early to Late Devonian range. The genus was originally described from Eifelian strata of the eastern Urals by Karpinsky (1884). Lyashenko (1958) significantly altered the diagnosis of the genus to include only smooth shells. Approximately ten European species are currently assigned to the genus; about half of these species were recognized after Lyashenko's redescription. Of the three species described from the Devonian of New York State by James Hall (1843, 1879, 1888), *S. spica* has been excluded from the genus and *S. obtusa* allied with the first described, and only assignable, North American species, *S. fissurella* (see Yochelson, 1986). Of the several European species described during the past century, at least four have also been placed in synonymy with *S. fissurella* (Bouček, 1964), and this makes the species the most abundant and cosmopolitan member of the genus.

Recent studies of *Styliolina fissurella* from eastern North America demonstrate that the outer surface is not smooth, but rather is incised by numerous sharp but shallow radial striae (Lindemann and Yochelson, 1984; Yochelson and Kirchgasser, 1986). Furthermore, it has been determined that the shell consists of a single layer of homogeneous calcite and is, therefore, fundamentally different from the laminated and multilayered shells of the nowakiids and other dactyloconarids (Yochelson and Lindemann, 1986). However, there has been no information on the microstructure of the type species *S. nucleata* (Karpinsky, 1884) from the Ural Mountains. It can now be confirmed that *S. nucleata*, as *S. fissurella*, has a shell that consists of homoge-

neous calcite. It is the purpose of this report to eliminate ambiguities that have engulfed the styliolines by providing a redescription of the genus based on topotypes of *S. nucleata* (Karpinsky, 1884). This study also offers an opportunity to redescribe *S. fissurella* (Hall, 1879) formally and to document the type collection.

Previous work

In his report on the Fourth Geological District of New York State, James Hall (1843) described a presumed echinoderm spine as *Tentaculites fissurella*. Hall (1879, p. 178) later assigned the species to the pteropod genus *Styliola*, and described the surface of the *Styliola fissurella* shell as "often smooth...and also with fine longitudinal striae."

Karpinsky (1884) proposed the genus *Styliolina* in order to distinguish these small conical fossils of the Paleozoic from the pteropod gastropods, and he assigned Hall's as *Styliola fissurella* to this new genus. He also described a new species, referred to *Styliola nucleata*, which Lyashenko (1958) later regarded as the type species of *Styliolina*. Fisher (1962) noted that this did not appear to be Karpinsky's intent. Karpinsky's thoughts regarding that species are ambiguous, as indicated by the fact that he did not assign the new species to *Styliolina*. Karpinsky even suggested that *Styliola nucleata* was conspecific with *Styliola obtusa* (Hall, 1879), which is now placed in subjective synonymy with *Styliolina fissurella* (see Yochelson, 1986).

Several investigators have also suggested that *Styliolina nucleata* and *S. fissurella* should be placed into synonymy (Fisher, 1962; Bouček, 1964; Lardeux, 1969). These points are significant in reevaluating the genus. Although the original description appears to have been disregarded in recent decades, Karpinsky (1884, p. 14) described *Styliolina* as "...glanzend, ganz sculpturlos oder mit Langsstreifen bedeckt." Clarke (1885, p. 57) translated Karpinsky's original text and noted that the description of the genus included "the presence of longitudinal incised lines." Clarke (1885) found this sculpture to be consistent with his observations on *Styliola fissurella* conchs. A later study by Grabau (1899, p. 282) assigned *S. fissurella* to *Styliolina* and described *Styliolina fissurella* as "sometimes [having] longitudinal striae." Despite these considerations, Lyashenko (1955) restricted the genus to species with smooth conchs. Following her opinions, a new genus *Striatostyliolina* and the Family Striatostyliolinidae (Bouček, 1964) were proposed to include those forms of conchs with longitudinal sculpture, usually ribs or lirae. Neither Lyashenko (1955) nor Bouček (1964) referred directly to the shell microstructure.

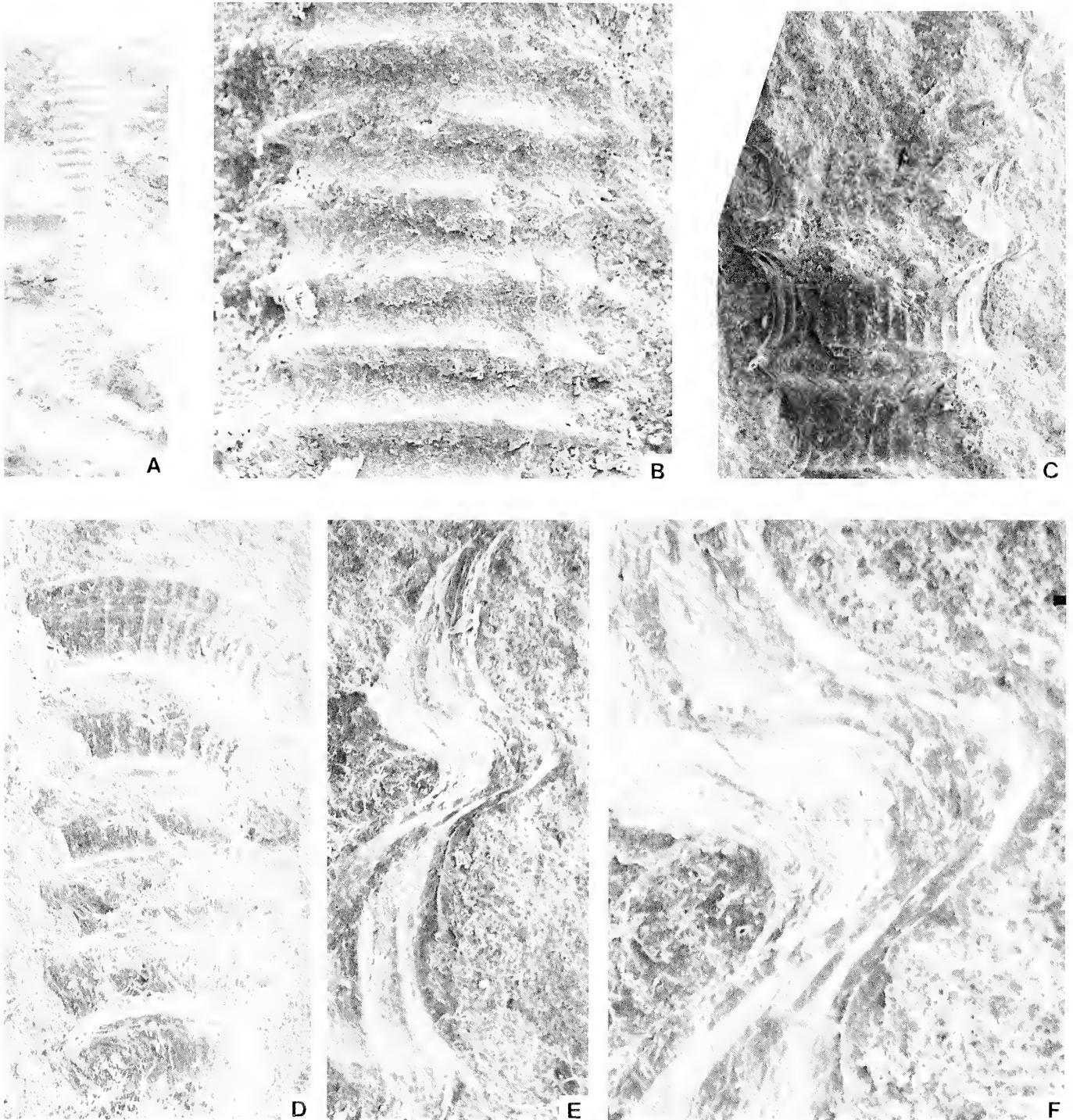


Plate 1. Nowakiids associated with *Styliolina nucleata*. *A*, Longitudinal view of Karpinsky's (1884) "*Tentaculites*" sp. indet., x40. Hematitic limestone, Pokrovskye, Russia, USNM No. 449189. *B*, Enlargement of Plate 1, Figure A, shows sharp-crested transverse rings and absence of longitudinal sculpture, x250. *C*, Longitudinal view of *Nowakia karpinskii*. Conch broken in the medial area shows a cross-section of the shell with three transverse rings and intervening depressions, x75. Hematitic limestone, Pokrovskye, Russia, USNM No. 449186. *D*, Longitudinal view of well-preserved *Nowakia karpinskii*, conch that shows transverse rings, growth lines, and longitudinal threads, x100. Hematitic limestone, Pokrovskye, Russia, USNM No. 449187. *E*, Enlargement of Plate 1, Figure C, shows foliated or finely laminated microstructure of the shell over a transverse ring and a swale, x200. *F*, Enlargement of Plate 1, Figure E, shows details of the finely laminated shell microstructure, x500.



Plate 2. Striatostyliolinids associated with *Styliolina nucleata*. *A*, Longitudinal view of conch from *Costulatostyliolina* sp. that shows prominent lirae, x75. Hematitic limestone, Pokrovskye, Russia, USNM No. 449191. *B*, Enlargement of Plate 2, Figure A, shows details of the lirae, weak transverse growth lines, and the laminated microstructure of the shell, x200. *C*, Enlargement of Plate 2, Figure A, shows inflation of the lirae at their intersections with the growth lines, x1,000. *D*, Longitudinal view of *Costulatostyliolina?* conch that is broken in the distal region, x100. Hematitic limestone, Pokrovskye, Russia, USNM No. 449192. *E*, Enlargement of Plate 2, Figure D, shows weak threads on the shell surface that are not visible at lower magnification, x400. *F*, Further enlargement of Plate 2, Figure D, demonstrates that neither diagenetic effects nor sample preparation have obliterated minute details of the shell surface, x1,000.

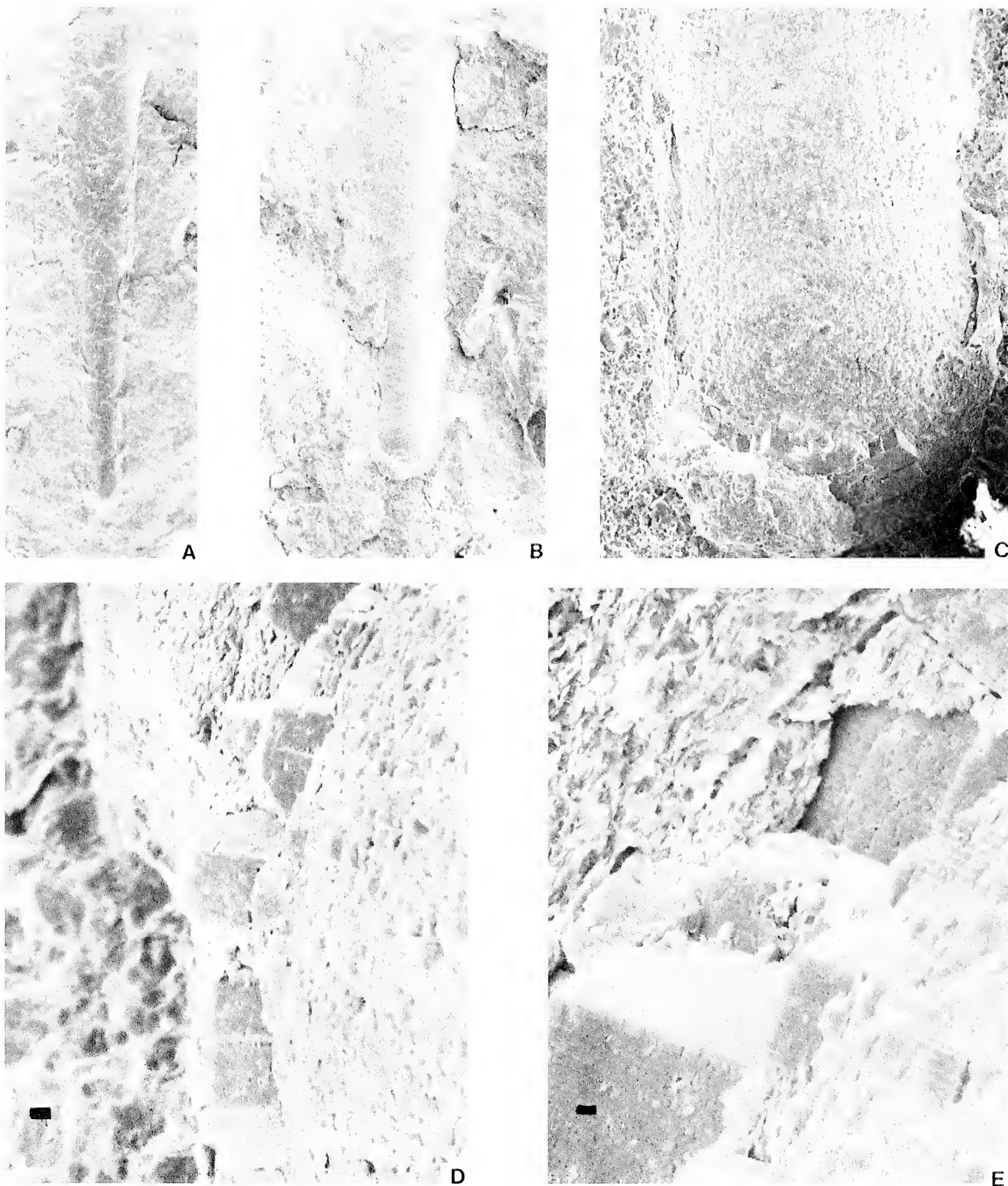


Plate 3. *Styliolina nucleata* topotypes. *A*, Longitudinal view of a complete and undeformed *Styliolina nucleata* conch, showing the rounded apical bulb and the growth angle, x50. Hematitic limestone, Pokrovskye, Russia, USNM No. 449190. *B*, Longitudinal view of a steinkern of *Styliolina nucleata* in the proximal and medial regions of the conch; most of the shell wall is broken away from the steinkern, but a small section of wall is exposed on the base of the rounded apical bulb, x75. Hematitic limestone, Pokrovskye, Russia, USNM No. 449193. *C*, Enlargement of Plate 3, Figure B, shows weak constriction between the apical bulb and remainder of the specimen, the rounded shape of the apical bulb, and the exposed shell at the base of the apical bulb; some sediment adheres to the shell exterior, x400. *D*, Enlargement of Plate 3, Figure C, from a different angle, steinkern to the right and matrix to the left, x1,500. *E*, Enlargement of Plate 3, Figure D, demonstrates that the shell consists of a single homogeneous layer, x4,000.

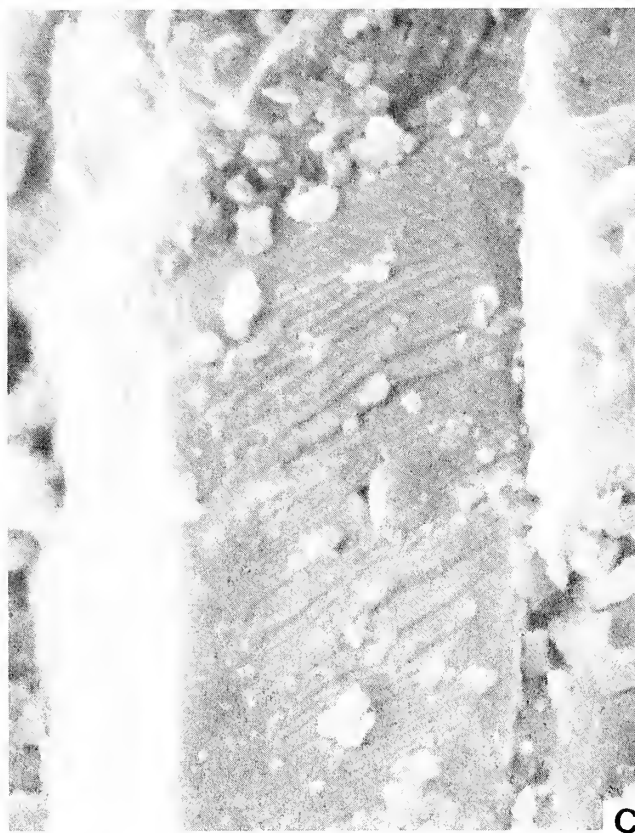
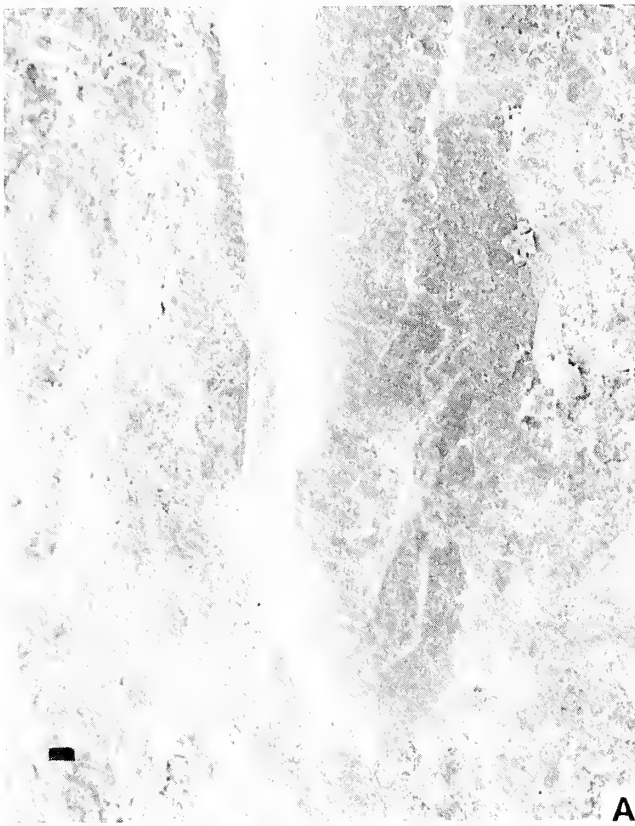


Plate 4. Details of the *Styliolina nucleata* conch compared with that of *Nowakia karpinskii*. A, Longitudinal view of apical region of a *Styliolina nucleata* conch shows rounded apical bulb with possible weak striae on the base of the bulb; elsewhere, most or all of the shell was detached from the steinkern during sample preparation, x250. Hematitic limestone, Pokrovskye, Russia, USNM No. 449188. B, Enlargement of Plate 4, Figure A, with a longitudinal section through the shell at the "neck" between the apical bulb and remainder of the specimen; although damaged, the homogeneous character of the shell is evident, x2,500. C, Enlargement of Plate 4, Figure B, demonstrates the microstructure of the shell, x10,000. D, Longitudinal section through the shell of *Nowakia karpinskii* showing oblique laminae for comparison with the homogeneous wall of *Styliolina nucleata* in Plate 4, Figure B, at the same magnification, x2,500. Hematitic limestone, Pokrovskye, Russia, USNM No. 449185.

There is confusion in the literature on the terminology of surficial sculpture, and this can be seen in the interchangeable use of the terms "striae" and "lirae" by some authors. "Striae" means radial grooves incised into the shell surface (Plate 6, Figures A-D). Their inverse, "lirae" or "threads," rise above the shell surface (Plate 2, Figures A-C). Both "striae" and "lirae" are radial on the shell surface and have a radial distribution on the circumference. A real confusion sometimes arises when one or the other of these features is very weakly developed (Plate 2, Figures D-F) and cannot be definitely resolved without the scanning electron microscope (SEM).

Bouček (1964) was the first to report the occurrence of *Styliolina fissurella* in the Devonian of Europe. On the basis of material recovered from shales and weathered limestones from Bohemia, he described the shell as smooth except for occasional growth lines, 10 mm or more in length, and with a shell wall 40-50 microns in thickness. Alberti (1975) illustrated the microstructure of *Styliolina* sp. from the Lower Devonian (Pragian) of West Germany. He described a shell that was 86 microns in thickness and composed of prismatic inner and outer calcite layers separated by a central nacreous layer. More recently, it was determined that the genus does not predate the Middle Devonian (Eifelian) in eastern North America (Lindemann and Yochelson, 1984), that the *S. fissurella* shell is uniformly 8-10 microns in thickness, and that it consists of a single layer of homogeneous calcite with numerous striae on the surface (Yochelson and Lindemann, 1986). Furthermore, *S. fissurella* and *S. nucleata* are usually only about 2 mm long and rarely exceed 4-5 mm (Hall, 1879; Karpinsky, 1884). These data indicate that fundamental characteristics of the genus, such as conch length, shell thickness, microstructure, and surface sculpture, have been variably interpreted during the last century. A correct diagnosis of the genus is resolvable only through restudy of *S. nucleata* Karpinsky.

Documentation and description of topotype *Styliolina nucleata*

Karpinsky (1884, p. 1, 15) described *Styliolina nucleata* from a single bed of red limestone that crops out at Pokrovskye on the eastern slopes of the central Urals. This locality is about 120 km northeast of Sverdlovsk in Russia. The available topotype suite is also in a red limestone from Pokrovskye. Among the macrofossils, Karpinsky (1884) mentioned the presence of orthoconic nautiloids; these are also present in our sample. In addition to *S. nucleata*, Karpinsky described and illustrated two tentaculitids: *Tentaculites acuarius* Richter, subsequently referred to *Nowakia karpinskii* by Lyashenko (1959), and *Tentaculites* sp. indet. Specimens of these are illustrated herein (Plate 1) to show the conspicuously foliated microstructure of *N. karpinskii* (Plate 1, Figures C-F; Plate 4, Figure D), and to document that our study material is identical to Karpinsky's (1884). However, it must be noted that Karpinsky's type specimens were not examined in this study, and the evidence for their existence is not available.

The study material originally consisted of several small pieces (ca. 0.9 kg) of red argillaceous and hematitic fossil packstone. The matrix is a subequal mixture of terrigenous mud and calcisilt. Quartz sand and silt are absent; glauconite is rare, and spherules of volcanic glass are common. There is no evidence of lamination or bioturbation, and the fossils show no preferred orientation. Nautiloids, gastropods, pelecypods, ostracodes, articulated brachiopods, pelmatozoan ossicles, rare trilobite fragments, nowakiids, styliolines, and plant fragments are all present. Many echinoderm and most molluscan allochems have thin

hematite coats, and the plant fragments are thoroughly permeated with hematite. Except for the echinoderms, nowakiids, and styliolines, virtually all of the fossils have undergone neomorphic alteration to pseudospar. Some of the nowakiids and most styliolines are in optical continuity with neomorphic spar and with their steinkerns (Plate 5, Figures E, F). About sixty specimens of *Styliolina nucleata* were exposed by repeated cracking of the sample; an additional thirty were studied in thin section.

The conch length ranges from 0.3-3.9 mm and averages just less than 2 mm in the topotypes of *Styliolina nucleata*. The apical bulb is 100-110 microns in diameter and 113-115 microns in length. This bulb is separated from the remainder of the shell by a long shallow constriction. The conch is approximately 10 microns less in width in the zone of constriction than the bulb diameter. The apex lacks a spine or node and is rounded in longitudinal section (Plate 3, Figures A-C; Plate 4, Figure A). The initial 7-10° growth angle of the shell diminishes to about 3° in the medial and distal regions of the longer specimens. Surficial striae, which are possibly a diagenetic feature, are observed only on the apical bulb of a single specimen (Plate 4, Figure A). Striae, growth lines, or other sculpture are not observed on the shell surface. Although the surfaces of some specimens were unquestionably modified by diagenesis or other taphonomic effects, the well-defined detail of the surficial sculpture on some *Costulatostyliolina* conchs (Plate 2, Figures B, C, E, F) suggests that the apparent lack of sculpture on *S. nucleata* surfaces is a primary feature. The shell consists of a single layer of homogeneous calcite (Plate 3, Figures C-E; Plate 4, Figures A-C; Plate 5, Figures E, F) that has a uniform thickness of about 10 microns along most of the length. Longitudinal sections through the conch (Plate 5, Figures E, F) show that the shell wall thins gradually and uniformly toward the aperture. The length over which the thinning occurs is a minimum of 150 microns.

Description of *Styliolina fissurella* and the illustrated type collection

The type locality for *Tentaculites fissurella*, Hall, 1843, cannot be determined precisely. In the original report, Hall (1843) figured specimens from the "Marcellus shale" and the "Genesee slate," and reported the species from localities throughout central and western New York. In the description of *T. gracilistriatus*, Hall (1879, p. 179) emphasized material from Alden, New York, particularly "an exposure of the Genesee slate, on the Cayuga Creek, two and a half miles southwest of Alden, in Erie County." It is significant that this quotation refers to a locality "southwest of Alden," not "near Alden" or simply "Alden." The American Museum of Natural History (AMNH) purchased Hall's collection, and its catalog of type specimens (Whitfield and Hovey, 1900, p. 326-327) refers the types of *Styliolina fissurella* and *Tentaculites gracilistriatus* to the "Genesee near Alden, N.Y." However, in 1843 and again in 1879, Hall used the locality designations "Alden," "near Alden," and "one-half mile east of Alden" interchangeably in referring to exposures of "Hamilton shale." This location is "On a small stream crossing the road near Alden, [where] the shales are well-exposed" (Hall, 1843, p. 190). In Hall's time, crossing the creek at this place would have interrupted travel and encouraged sampling where outcrops immediately flank the area of the ford.

Whitfield and Hovey (1900) cataloged specimens that are now assigned to AMNH numbers FI 5830 A, B, C, and D. These were regarded as the syntypes of *Styliolina fissurella*, which were illustrated by

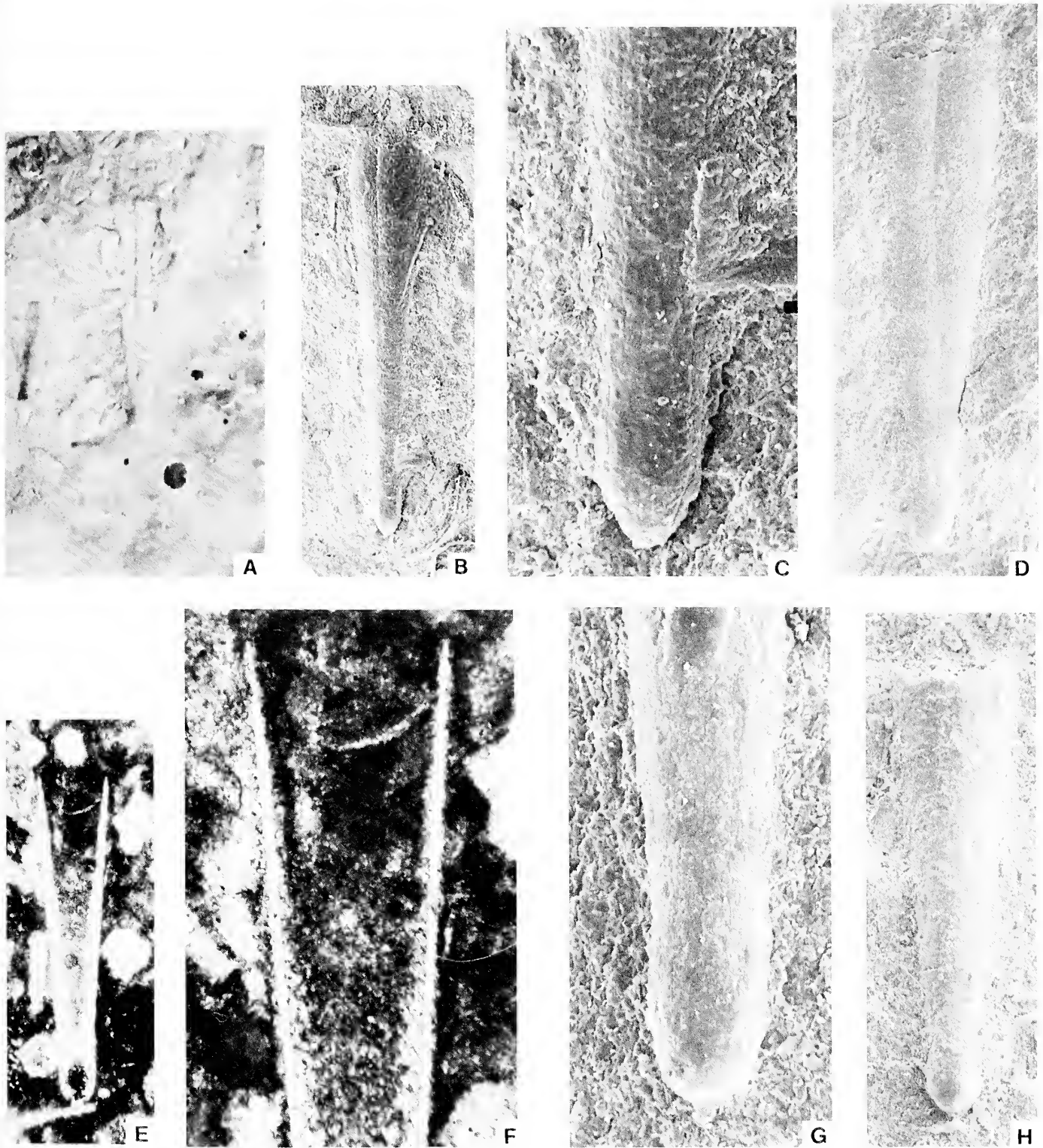


Plate 5. *Stylioline fissurella* lectotype, details of the *S. fissurella* shell, and a thin section of *S. nucleata*. **A**, The *Stylioline fissurella* lectotype. The shell is compressed and the apical region obscured by glue used to secure the paper diamond that locates the specimen, x15. Ledyard Member, Ludlowville Formation, Alden, New York. AMNH No. FI 5830B. **B**, Characteristic conch of *S. fissurella*, partially compressed, x50. Wanakah Member, Ludlowville Formation, from a weathered bank on the north side of a stream, 100 m east of Francis Road and 0.5 km south of the Delaware, Lackawanna, and Western railroad, 3.4 km northwest of Bethany Center, Batavia South 7 1/2-minute Quadrangle, Genesee County, New York. USNM 376771. **C**, Enlargement of Plate 5, Figure B, shows the shape of the apical bulb and surficial striae, x200. **D**, A complete specimen of compressed *S. fissurella* conch, x75. Ledyard Member, Ludlowville Formation, from the type locality on Spring Creek, east of Alden, New York. USNM 449195. **E**, Longitudinal thin section through conch of *S. nucleata* in plane light, x55. Hematitic limestone, Pokrovskye, Russia, USNM No. 449194. **F**, Enlargement of the apertural region of Plate 5, Figure E, shows shell wall of uniform thickness in optical continuity with surrounding sediment and steinkern, as well as gradual thinning of the shell near the aperture, x150. **G**, Apical bulb and proximal region of *S. fissurella* with weak surficial striae, x200. Horizon and locality as Plate 5, Figure D. USNM 449230. **H**, *S. fissurella*, conch, slightly compressed and broken at the aperture, x75. Horizon and locality as Plate 5, Figure B. USNM 376768.

Hall (1879) on Pl. 31A, Figs. 13, 30, 23, and 24, respectively. Direct comparison between the specimens and their respective illustrations confirms that the figure numbers on the labels are correct. The exception is specimen AMNH FI 5830A, which Hall (1879) apparently did not figure.

Specimen AMNH FI 5830B has a diamond-shaped paper frame that surrounds a *Styliolina fissurella* conch that was illustrated by Hall (1879, Pl. 31A, Fig. 30). Several additional conchs that Whitfield and Hovey (1900) did not number also occur within this paper frame. One of these is more or less surrounded by blotches of a green paint-like substance, and this suggests that it may have received special attention.

This second conch on AMNH FI 5830B is very similar to the *Styliolina fissurella* specimen illustrated by Hall (1879) on his Plate 31A, Figure 29. Hall's (1879) caption notes that the specimens illustrated on Figures 29 and 30 of Plate 31A are located on the same slab, and this is further evidence that this second conch is a hitherto unrecognized syntype of *S. fissurella*.

However, this specimen, as well as AMNH FI 5830A (not figured by Hall, 1879) and AMNH FI 5830C and D (Hall, 1879, Pl. 31A, Figs. 23 and 24, respectively), are not referable to *Styliolina fissurella*. All of these specimens have the weak lirae and transverse undulations of *Viriatellina* Bouček (1964). This means that only one specimen of the type collection, AMNH FI 5830B, is referable to *S. fissurella* (Hall). In conclusion, this specimen (Plate 5, Figure A) is designated herein as the lectotype of *S. fissurella*. No paralectotypes are present among Hall's illustrated types of *S. fissurella* because they are referable to *Viriatellina*.

The slab bearing specimens AMNH FI 5830 A, B, C, and D is a dark grey shale, roughly ovoid in outline, that measures 17 cm by 12 cm. Glued to the reverse side is a white paper tag with "1/2 M.E. [sic] Alden" handwritten in black ink. This site designation is not an erroneous abbreviation for "northeast;" it is an abbreviation for "Mile East." It specifically locates the stream crossing referred to by Hall (1843, p. 190), which is precisely 0.5 mile east of the center of Alden, New York. The original tag does not mention the stratigraphic unit from which the slab was collected, although old and new typed labels for the slab refer it to the "Genesee slate" located "1/2 M.E. of Alden." Unfortunately, the slab is lithologically and paleontologically very different from the Genesee Shale. Furthermore, the geologic map of Erie County, New York (Buehler and Tesmer, 1963), does not show the Genesee Shale outcrop belt anywhere near, and certainly not 0.5 mile east, of Alden, New York. The area in and around Alden is in the outcrop belt of the Ludlowville Formation.

The Corfu, New York, 7 1/2-minute Quadrangle indicates that New York Rte. 20, the road to which Hall (1843, p. 190) referred, crosses Spring Creek 0.5 mile east of the center of Alden, New York. Intermittent outcrops in the creek banks are in the Ledyard Member of the Ludlowville Formation. Known for its Alden Pyrite Bed (Babcock and Speyer, 1987), the Ledyard is predominantly an interval of dark grey shales in its lower part and medium grey, calcareous, finely laminated shales in its upper part (see McCollum, 1991). Immediately adjacent to Rte. 20, and particularly in the area 100-300 m upstream from the road, is an exposure of a 20-30 cm interval of more thoroughly indurated, medium to dark grey, calcareous shale in the bank of Spring Creek. This indurated shale occurs 1.4 m below the "Athol Springs bed" (Kloc, 1983, = "pteropod bed" of Cooper, 1930) and approximately 5.9 m above the Alden Pyrite Bed. Samples from this interval bear a strong resemblance to Hall's slab that has specimens AMNH FI 5830 A, B, C, and D. This bed is designated as the topotype interval for *Styliolina fissurella* (Hall) because this is unquestionably the type local-

ity, and no other strata exist in the Ledyard, at this locality, with a lithology similar to this slab.

There is considerable variation between the exterior surfaces of *Styliolina fissurella* conchs, particularly when observed under moderately high magnification. Some specimens are obviously sculptured; others are not. Radial striae are evident on some specimens and encircle the conch (Plate 5, Figure C; Plate 6, Figures A-D). They extend from the tip to the aperture of the conch. Precise counts are difficult to make, but between thirty and fifty striae occur around the conch. The striae, although sharp, are incised only a very short distance into the shell. Their shallow depth is obvious in oblique views of a broken section. This explains their apparent absence on many specimens. Some specimens show striae disappearing into weathered or etched areas of the surface (Plate 6, Figure D), whereas others show slightly weathered surface patches that are not striated (Plate 5, Figures C, G).

Observations of longitudinal thin sections through *Styliolina fissurella* conchs demonstrate that the shell is uniformly about 10 microns thick over most of its length (Yochelson and Lindemann, 1986, Figs. 1, 2). The shell thins only slightly in the distal 50-80 microns near the aperture. Numerous broken sections have been observed, and they, too, are through conchs with uniform thickness that are internally homogeneous with no obvious layers or laminae within the shell (Plate 6, Figures A, B; Plate 7, Figures A-D). The homogeneous character of the shell has also been observed in transverse section (Yochelson and Lindemann, 1986, Fig. 4).

Systematic paleontology

Phylum, Class, and Order INCERTAE SEDIS

Family STYLIOLINIDAE Grabau and Shimer, 1910

Included genera.—*Styliolina* Karpinsky, 1884, is the only genus assigned to the family.

Remarks.—Lyashenko (1958) cited Grabau (1912) as the original author of this family, a reference that Fisher (1962) could not confirm. No publication that matches this reference was located in the course of this study. However, Grabau and Shimer (1910, p. 15, 16) referred to the Styliolinidae, referred to "*Styliolina* Karpinsky," and illustrated specimens of *S. fissurella* (Hall).

Lyashenko (1958) and Bouček (1964) both utilized sculpture of the shell surface as a principal feature for discriminating taxa at the familial level. Bouček also regarded shell microstructure as a principal feature for ordinal determinations; unfortunately, he did not have access to scanning microscopy techniques, and he believed the stylioline shell to be laminated in the manner of the nowakiids. Yochelson and Lindemann (1986) determined that the shell of *Styliolina fissurella* consists of a single layer of homogeneous calcite, and regarded this to be a diagnostic feature of the Styliolinidae. It was determined in the course of this study that the wall of the *S. nucleata* conch is essentially identical to that of *S. fissurella*. It was also determined that the walls of the nowakiids (Plate 1, Figure F; Plate 4, Figure D), as well as *Metastyliolina* and *Costulatostyliolina*, are laminated and/or layered (Plate 2, Figures A, B), but information on *Striatostyliolina* is not currently available. Thus it is premature to redescribe the Styliolinidae formally. However, Bouček's (1964) determination that shell microstructure is significant at high systematic levels is probably accurate. Because the styliolines are fundamentally distinct from the tentaculitids and nowakiids in this feature (Yochelson and Lindemann, 1986), this family is not assigned to any higher taxon in this report.

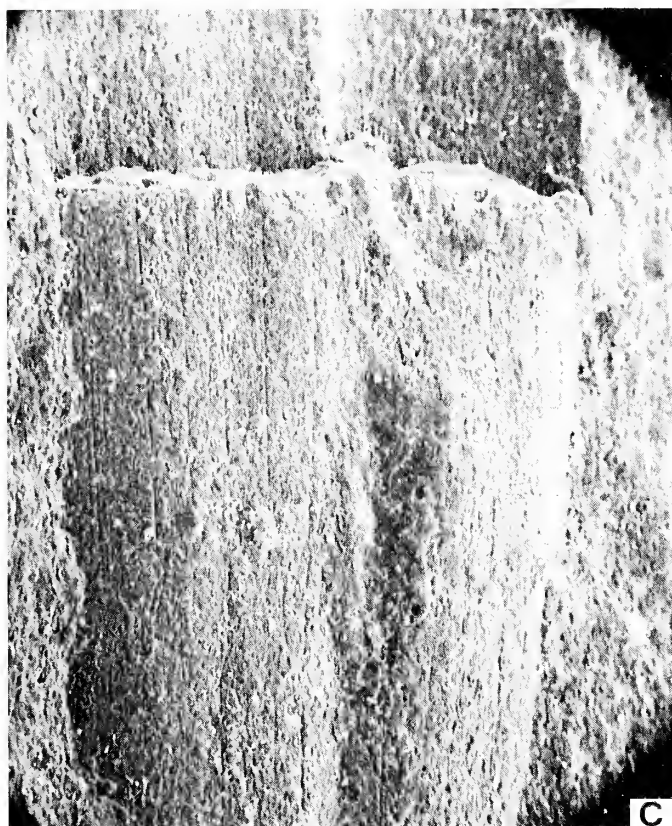


Plate 6. Details of the *Styliolina fissurella* shell. *A*, Well-preserved specimen with surface striae and a partial surface of the steinkern, x100. Rhinestreet Shale, West Falls Formation. From a small tributary to Cazenovia Creek, approximately 4.0 km south of Springbrook, Springville 15-minute Quadrangle, Erie County, New York. USNM No. 449196. *B*, Enlargement of Plate 6, Figure A, shows that the striae are only slightly incised into the shell surfaces and that the shell has a homogeneous microstructure, x250. *C*, Crushed specimen with weak striae on the shell surface, x150. Genesee Shale, Genesee Formation. USGS locality 10567-SD, USNM No. 398489. *D*, Undeformed specimen with striae that vanish into a slightly weathered area of the shell surface, x200. Genesee Shale, Genesee Formation. USGS locality 10565-SD, USNM No. 398493.

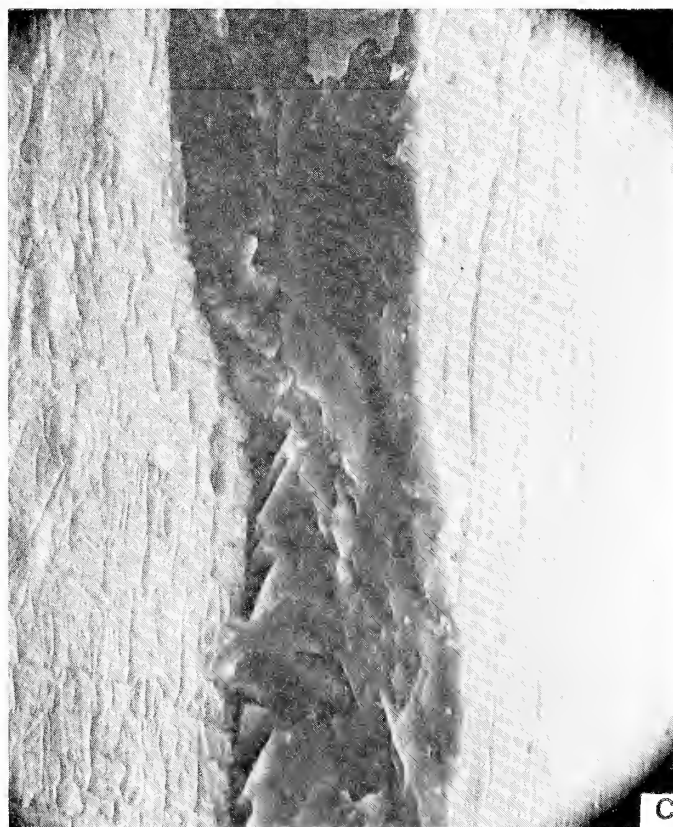


Plate 7. Homogeneous shell microstructure of *Styliolina fissurella*. A, Longitudinal view of several imbricated specimens, x35. Genundewa Limestone, Genesee Shale. USGS locality 10567-SD, USNM No. 449197. B, Enlargement of the medial region of the central specimen in Plate 7, Figure A, x250. C, Enlargement of Plate 7, Figure B, shows the steinkern surface (on left), weak striae on the shell surface (on right), and a longitudinal section through the shell, x1,000. D, Enlargement of Plate 7, Figure C, demonstrates that the shell consists of a single homogeneous layer, x3,000.

Genus STYLIOLINA Karpinsky, 1884

Type species.—*Styliola nucleata* Karpinsky, 1884

Diagnosis.—Small organisms known from straight, slender, nonseptate, conical shells composed of a single, uniform, homogeneous calcite layer; conch exterior may appear smooth or, less commonly, have weak radial striae; the apical bulb is confluent with the apical part of the conch, rounded to slightly conical or blunt-ended, lacks a spine or other protuberance, and is separated from the cone by a slight constriction of the shell; aperture simple and transverse.

Included species.—*Styliolina nucleata* and *S. fissurella* (Hall, 1879).

Remarks.—Numerous species have been assigned to this genus (see Bouček, 1964, p. 124-131) on the basis of poorly preserved or poorly documented material and without the aid of the scanning electron microscope to discern minute details of shell sculpture and microstructure. Alberti (1975) described the microstructure of a presumed *Styliolina* sp. that differs radically from that of *S. nucleata* and *S. fissurella*. It has been determined herein that topotypes of the type species *S. nucleata*, as well as topotypes of *S. fissurella*, have a shell wall that consists of a single thin layer of homogeneous calcite, and it is concluded that this structure is fundamental to the genus. It has also been determined that striae are present over the full length of *S. fissurella* and perhaps on the apical bulb of *S. nucleata*. For these reasons, a conservative approach to inclusion of additional species is taken, and opinion is reserved on all others until each species is individually evaluated for shell surface details and shell microstructure.

Stratigraphic range.—Middle Devonian (Eifelian) to Upper Devonian (Frasnian).

STYLIOLINA NUCLEATA Karpinsky, 1884

Plate 3, Figures A-E; Plate 4, Figures A-C; Plate 5, Figures E, F
Styliola nucleata KARPINSKI, 1884, p. 14-15, Figs. 15-19.

Proposed diagnosis.—*Styliolina* species known from conchs up to 4-6 mm long and with an apical angle of $7-10^\circ$; conchs become subcylindrical in the medial and distal regions; apical bulb 0.13-0.15 mm long, 0.1-0.11 mm wide, set off from the rest of the conch by a slight constriction of the shell; shell surface possibly with weak striae, although usually appears smooth; shell wall of homogeneous calcite, uniformly 10-12 microns thick in the proximal and medial regions, and thins aperturally over a length of more than 150 microns to the otherwise undifferentiated aperture.

Material.—Approximately sixty partial and complete topotypes from a Middle Devonian (Eifelian) hematitic limestone at Pokrovskye, in the east-central Ural Mountains.

Discussion.—Although a few other descriptions of *S. nucleata* are in the literature, none consider the shell microstructure. These references have been omitted from the synonymy.

STYLIOLINA FISSURELLA (Hall, 1843)

Plate 5, Figures A-D, G, H; Plate 6, Plate 7

Tentaculites fissurella HALL, 1843, p. 182, figs. 71, 94.

Styliola fissurella HALL, 1879, p. 178-179, Pl. 31A, figs. 7, 9, 12, 22, 26-28, 30, 47 (?figs. 5, 6, 8, 10, 11, 16-20, 31-33) [not Figs. 1-4, 13-15, 23, 24, 29].

Styliola obtusa HALL, 1879, p. 182, Pl. 31A, figs. 34-36.

not *Styliolina fissurella* (Hall). BOUČEK, 1964, p. 128-129, Pl. 13, figs. 1-2; Pl. 32, figs. 3-9.

Proposed diagnosis.—*Styliolina* known from conchs up to 5 mm long with an apical angle of $5-7^\circ$; conchs become subcylindrical in the medial and apertural regions; the closed, teardrop-shaped apical bulb is

0.12-0.17 mm long, 0.09-0.14 mm wide, set off from the cone by a broad shallow depression; shell surface with numerous weak striae and rare transverse growth lines, although it often appears featureless; shell wall of homogeneous calcite, uniformly 8-10 microns thick in the apical and medial regions and thinning slightly 50-80 microns from the aperture; aperture simple and transverse.

Comparison and relations.—*Styliolina fissurella* appears worldwide in Devonian faunal lists. Unfortunately, Bouček (1964) did not have access to scanning microscopy and could not provide descriptions of the European specimens that are adequate for positive identification. This report is concerned only with type and topotype specimens; additional citations are not included in the synonymy list.

Styliolina fissurella is so similar to *S. nucleata* that virtually all investigators of the taxon have suggested synonymy (Karpinsky, 1884; Fisher, 1962; Bouček, 1964). Although there are minor differences, such as the distance over which the shell thins, with the conch of *S. fissurella* thinning more abruptly in the apertural region than that of *S. nucleata*, a definite similarity exists between the two species.

It is very difficult to differentiate species of such simple architecture solely on the basis of physical criteria. However, differences in apparent habitat preference provide a quite-compelling argument for their distinction. *Styliolina fissurella* is abundant in open-shelf facies, rare to absent in nearshore sediments, and is associated commonly with *Viriatellina gracilistriata* (Hall), a species unknown in Europe and Asia. On the other hand, the occurrence of *S. nucleata* in hematitic limestone rich in plant fragments suggests a nearshore or transitional habitat, and this species is associated with *Nowakia karpinskii* (Lyashenko) and other species unknown in North America. Furthermore, *S. fissurella* and *S. nucleata* occur in different faunal provinces that did not tend to share dacryoconarid taxa during the Middle Devonian. It is possible that pronounced differences in geographic occurrence, habitat preference, and associated faunas are indicative of an underlying genetic differentiation between these two species.

Material.—Lectotype AMNH FI 5830B (Hall, 1879, Pl. 31A, fig. 30) and several dozen specimens on this slab from the Ledyard Member of the Ludlowville Formation; the locality is on the Corfu, New York, 7 1/2-minute Quadrangle along Spring Creek at its intersection with New York Rte. 20, 0.5 mi. east of Alden, New York. Numerous topotypes have been collected.

Occurrences.—The species has been confirmed in New York from the lower Eifelian Edgecliff Member of the Onondaga Limestone (Lindemann and Yochelson, 1984), and ranges up through the late Frasnian Angola Shale of the West Falls Formation (Yochelson and Kirchgasser, 1986). All other reports of younger occurrence are suspect and require confirmation.

Acknowledgments

This research would have been impossible without the cooperation of B. Chuvashov, Institute of Geology and Geochemistry, Academy of Sciences, Sverdlovsk, Russia. Dr. Chuvashov generously responded to our request for topotype material. N. Eldredge, American Museum of Natural History, New York City, allowed us to borrow types in his charge. G. Kloc, University of Rochester, provided specimens and invaluable field assistance in determining the type stratum of *Styliolina fissurella*. W. Kirchgasser, State University of New York College at Potsdam, also provided assistance in the field. K. Szymborski, S. Webb,

and M. Sheffer of the Scribner Library, Skidmore College, helped obtain reference materials. W. Brown and the other members of the SEM Laboratory staff at the National Museum of Natural History provided the photographs. R. Feldman and J. Hannibal reviewed the manuscript. RHL personally supplied \$140 toward publication of this report.

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Revised stratigraphic and facies relationships of the lower part of the Clinton Group (middle Llandoveryan) of western New York State

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Abstract

The lower part of the Clinton Group (Lower Silurian, Llandoveryan) of western New York State and adjacent Ontario is an unconformity-bounded sequence composed of alternating greenish grey to purplish shale, fossiliferous carbonates, and thin hematites. Successively older Clinton units are beveled in a westward direction beneath a major unconformity at the middle of the Clinton Group (sub-Williamson unconformity). The three lower formations (the Neahga and Maplewood Shales and the Reynales Limestone), which alone persist into Orleans and Niagara Counties, are the subject of this paper. The base of the Clinton Group (emend.) can be drawn unambiguously at a thin phosphatic conglomerate bed (Densmore Creek Bed, new unit) that unconformably overlies pale greenish grey to white (leached) sandstones and shales of the Kodak and Thorold Formations. Although the latter units have formerly been correlated with and included in the Clinton Group, they are herein separated and assigned to the underlying Medina Group (emend.). The Densmore Creek Bed forms the base of both the Neahga (grey) and Maplewood (greenish grey) Shales; this evidence suggests that these units are precisely correlative. These shales accumulated in shallow, partially partitioned basins separated by a local, northeast-trending high area that crops out near Lockport, New York. The Maplewood Shale also pinches out abruptly into a complex, hematitic, multigenerational phosphatic conglomerate bed (herein termed the "Webster Bed") along a line extending southwest from eastern Monroe County.

The base of the overlying Reynales Limestone (Brewer Dock Member) is also marked by a widespread, thin phosphatic bed (Budd Road Bed, new unit); this horizon may represent a significant unconformity. The Brewer Dock Member of the Reynales Limestone is a thin (0.5 to 1.0 m) interval composed of three carbonate packstone-to-green-shale, upward-shallowing cycles. The top of the unit is marked locally in Monroe County by a fossiliferous hematitic limestone, the Seneca Park Bed (new unit). The Brewer Dock Member passes eastward into a hematitic limestone and shale interval (Furnaceville Member, emend. herein) of comparable thickness. The overlying 5.0 to 6.0 m-thick Wallington Member also contains several widely traceable carbonate-to-shale cycles that facilitate very detailed correlations eastward into the coeval Bear Creek Shale.

At least three scales of cyclicity (probably 4th- to 6th-order cycles) occur in the lower part of the Clinton Group. Detailed correlation of facies within the minor cycles indicates a relatively consistent pattern of east to west bio- and lithofacies changes. The easternmost quartzose

phosphatic conglomerates represent shoreline facies, and pass westward (offshore) into greenish grey shales with an *Eocoelia*-dominated biofacies (benthic assemblage 2 or BA-2). These shales, in turn, give way to pelletal grainstones and pentamerid- (or *Hyattidina*-) rich crinoidal packstones and grainstones (shoal facies, BA-3), and finally to nodular, bryozoan-rich wackestones (BA-4). Detailed facies transects provided by the microstratigraphy of the lower part of the Clinton Group corroborate models of benthic assemblage distribution and provide insight into Silurian biofacies.

Introduction

The Clinton Group (Lower Silurian) of western New York is a thin but complex interval with numerous lithofacies that includes hematitic oolitic iron ore, green shales, phosphatic beds, and coquinoid limestones (Gillette, 1947). Laterally, this interval exhibits a relatively complete facies spectrum from nearshore conglomerates to deeper-shelf facies. At least three scales of cyclicity are present in this thin interval, and the Clinton Group provides key insights into lithofacies cycles within the Silurian. Gillette (1947) informally subdivided the Clinton Group into Lower, Middle, and Upper portions on the basis of discontinuities in ostracode biostratigraphy. Recent work reinforces the utility of this subdivision. In particular, Gillette's units appear to represent unconformity-bounded sequences sensu Vail et al. (1977; see Brett et al., 1990a, 1990b). This report concerns detailed stratigraphy and facies relationships within the lower part of the Clinton Group, or "Lower Clinton Group" of Gillette (1947).

Although the lower part of the Clinton Group (Lower Silurian, Llandoveryan) in the Rochester to Niagara area has been studied intensively for over a century, a number of subtle relationships have remained unresolved. Fisher (1953a) made the last detailed study of the lower part of the Clinton Group, and described several aspects of the regional stratigraphy in the area between the Niagara Gorge and the Genesee Gorge.

In New York State, the "Lower Clinton Group" attains a maximum thickness of approximately 50 m in the Wayne County area. This interval includes, in ascending order, the Maplewood Shale (or equivalent), Reynales Limestone, "Lower" and "Upper" Sodus Shales, and Wolcott Limestone. The lower part of the Clinton Group is represented in central Pennsylvania by over 80 m of purple and greenish shale that composes the lower part of the Rose Hill Formation. This interval of the Rose Hill corresponds to the *Zygobolba emaciata*, *Z. anticostiensis* (=Z.

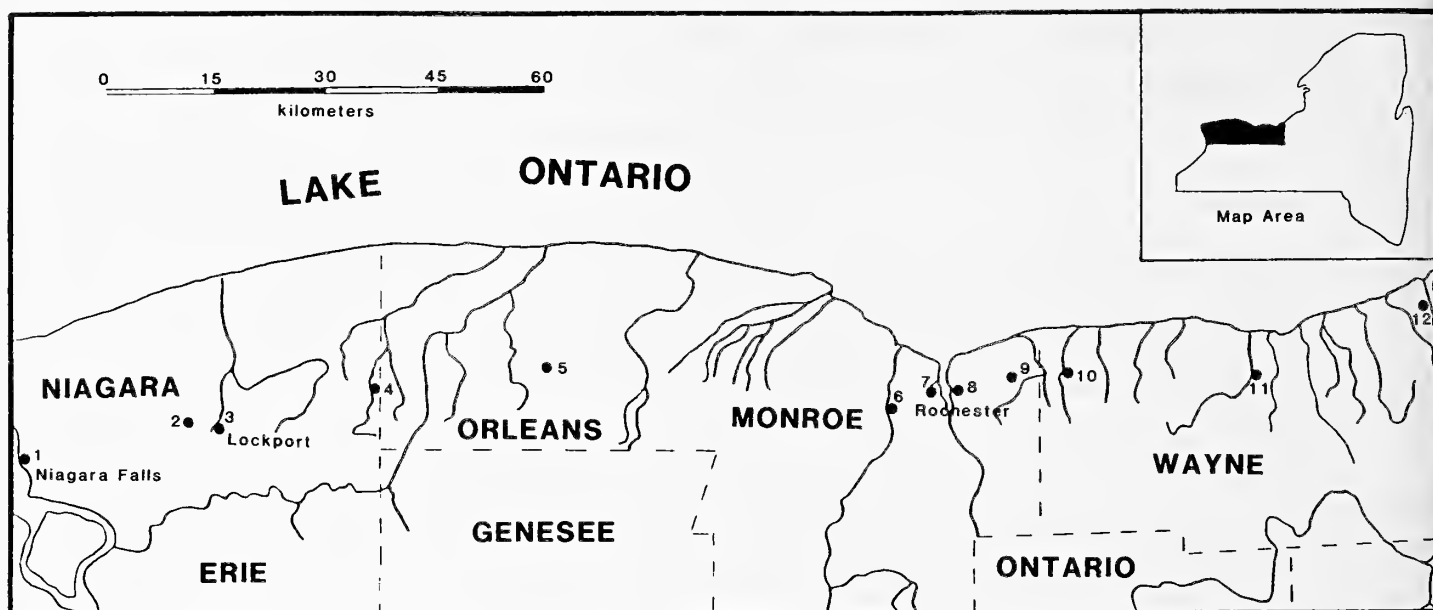


Figure 1. Location map of the study area showing outcrops and drill cores of the lower part of the Clinton Group. Note location of counties referred to in text.

excavata), and *Z. decora* Zones (ostracodes). The lower part of the Clinton Group in western New York represents only part of this sequence, and is equivalent to the lower portion of the *Zygobolba excavata* Zone. Conodont biostratigraphy in this interval remains somewhat uncertain.

This report stems from several new discoveries within the "Lower Clinton Group" that resulted from reexamination of outcrops, extensive drilling in Niagara and Monroe Counties, and test drilling in Orleans and Wayne Counties (Figure 1). These activities provided new data upon which to base the revised correlations.

Fisher (1953a) recognized, as Gillette (1947) had earlier, that the upper portions of the "Lower Clinton Group" ("Lower" and "Upper" Sodus Shales and Wolcott Limestone) were absent in western New York. Recent study (Lin and Brett, 1988) revealed that the upper surface of the "Lower Clinton Group" lies at a distinct regional angular unconformity; moreover, this surface has been proposed (Brett et al., 1990a, 1990b) as a major erosive sequence boundary associated with a late Llandoveryan (late C-5 to earliest C-6) sea-level lowstand and coincident with minor tectonism on the Algonquin Arch forebulge. This surface progressively bevels strata in the lower part of the Clinton Group, and actually merges with a sub-Clinton erosion surface that truncates the upper part of the Medina Group in the vicinity of St. Catharine's, Ontario (Figures 2, 3). In western New York and the easternmost Niagara Peninsula of Ontario, only a very small fraction of the "Lower Clinton Group" is available for study. It cannot be proven that higher Clinton strata were ever deposited in this region; however, there is some indication that these units once may have extended at least to Rochester. Gillette (1947) reported the discovery of limestone clasts that closely resemble the Wolcott Limestone on the erosion surface beneath the Williamson Shale at the Genesee Gorge in Rochester. There is no evidence of internal thinning or condensation of units in the lower part of the Clinton Group as they approach their westward erosional terminus. This also points to the probability that these units once extended substantially westward prior to regional uplift in the area that extends from central New York State to Hamilton, Ontario. Furthermore, it recently

has been suggested that the western equivalent of much of the lower part of the Clinton Group reappears beneath the C-6 erosion surface in the vicinity of the Bruce Peninsula of Ontario, where the Dyer Bay, Wingfield, and St. Edmund Formations successively appear northward beneath the (Llandoveryan C-6) Fossil Hill Formation (Colville and Johnson, 1982; Brett et al., 1990a, 1990b). These units appear to correspond approximately to the Reynales, "Lower" Sodus, "Upper" Sodus, and Wolcott Formations in New York State (Figure 2). Thus the upper surface of the "Lower Clinton Group" appears to be a regional angular unconformity. Unfortunately, the removal of all "Lower Clinton Group" units in southern Ontario precludes complete lateral facies analysis of these formations. However, the lowest beds can be traced west to St. Catharine's, and provide some insights into regional paleogeography and facies distribution.

The base of the Clinton Group also lies at a regional angular, although minor, truncation surface marked by a persistent phosphatic bed (Brett et al., 1990b) that was previously recognized and mapped, in part, by Fisher (1953a; herein designated the "Densmore Creek Bed," Figure 4). Contrary to previous assertions, the sandstone beneath this phosphatic bed is not conformable with overlying strata. Furthermore, the pale greenish grey sandstone that underlies the Clinton Group in western New York and Ontario is not a single, correlative unit. The white to greenish Kodak Sandstone beneath the shales in the lower part of the Clinton Group in the Genesee Gorge area in Rochester does not appear to be correlative with the somewhat similar Thorold Sandstone, that underlies the same shales to the west. Rather, the Kodak Sandstone, and 5.0 to 7.0 m of underlying red and greenish mudstone ("Cambria Shale," designation herein), are beveled beneath the basal Clinton unconformity, and the Thorold itself is truncated west of Grimsby, Ontario. Hence this is another low-angle regional unconformity, and forms a lower sequence boundary.

As a result of these two surfaces, the "Lower Clinton Group" is stratigraphically bounded and can be considered as a sequence in the sense of seismic stratigraphers (Figure 3). In a recent report (Brett et al., 1990b), the Medina Group has been designated as sequence I and the lower part

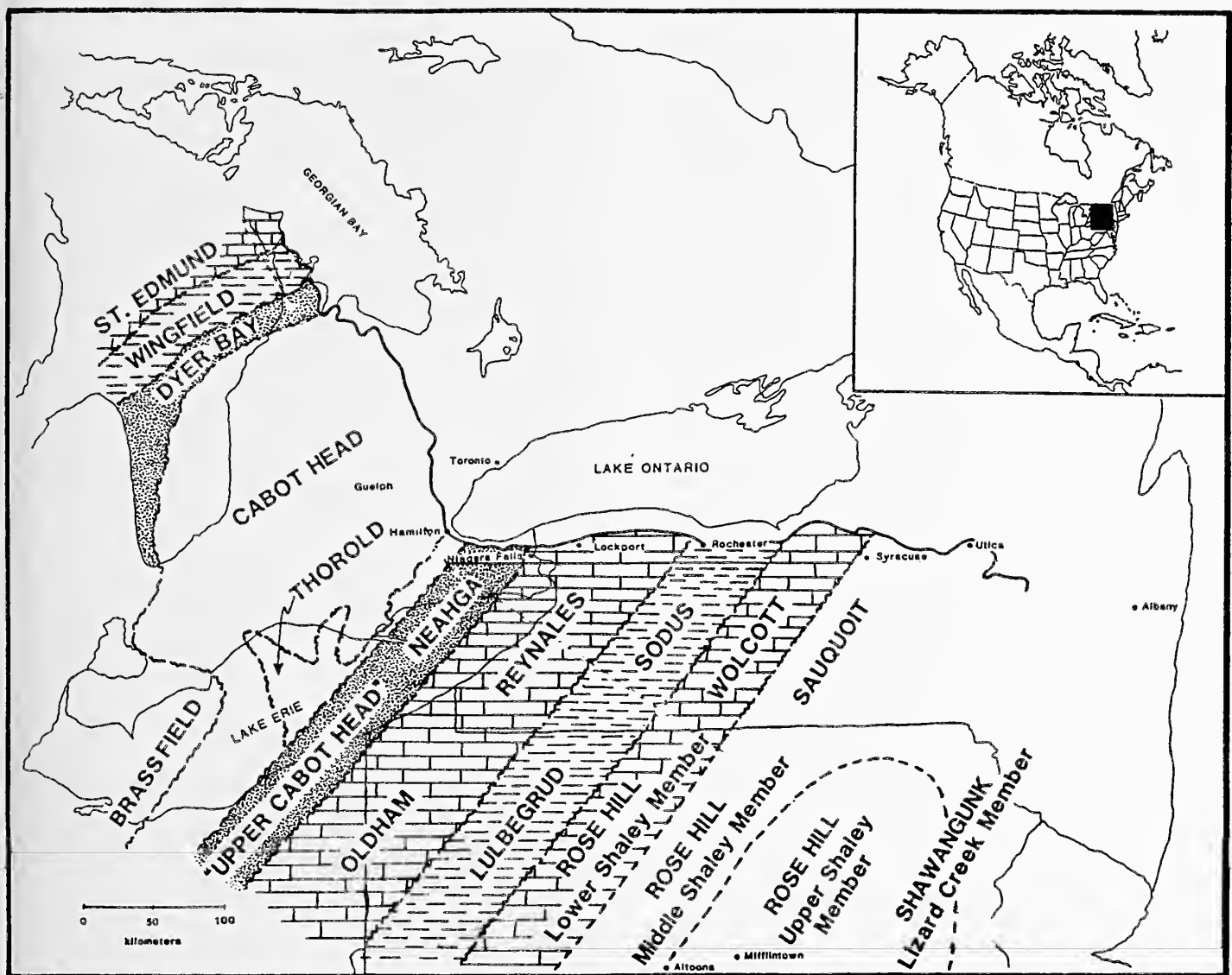


Figure 2. Subcrop map of Silurian units at regional angular unconformity underlying Llandoveryian C-6-age strata (Fossil Hill–Merrittton Limestones in Canada; Williamson–Willowvale Shales in New York). Note the westward beveling of lower units of the Clinton Group (shaded) in western New York and southern Ontario, and the appearance of possibly coeval strata to the north along the Bruce Peninsula. Area of maximum removal of strata near Hamilton, Ontario, corresponds to the Algonquin Arch (modified from Brett et al., 1990a).

of the Clinton Group as sequence II; the lower part of the Clinton Group is unconformably overlapped by the Sauquoit Formation along a phosphatic conglomeratic bed that marks a third sequence boundary. Westward, the Sauquoit Formation is truncated by the upper erosion surface beneath the Williamson–Willowvale Formations, and the two unconformities merge into one that overlies the “Lower Clinton Group.”

Sub-Clinton stratigraphy

Underlying units

Traditionally, the base of the Clinton Group has been drawn at the base of the so-called “Thorold Sandstone.” Gillette (1947) and Fisher (1953a) both agreed that the “Thorold” is an extensive, thin (0.7 to 3.0 m), pale grey to greenish sandstone that represents reworked sand can-

nibalized from the underlying Medina Group. They implied that the “Thorold” was a sheet-like transgressive deposit with a sharp base and was conformable with the overlying Maplewood or Neahga Shale. The so-called “Thorold,” or “grayband,” was traced from the type area near Thorold, Ontario, eastward at least to western Oswego County, where the unit was believed to merge into the Oneida Conglomerate. Gillette (1947) indicated that this unit belonged to the *Zygobolba excavata* ostracode Zone of the lower part of the Clinton Group. However, the only ostracodes actually found within the so-called “Thorold” interval were nondiagnostic leperditians. Only in some of the eastern localities, where the “Thorold” was said to merge with the Oneida Conglomerate, were zonally significant *Zygobolba* species recovered (see Gillette, 1947, p. 29). Furthermore, the ostracodes were from shale partings in the Oneida, and the latter apparently is separated from the Medina Group by an unconformity.

New observations in the lower part of the Clinton Group and the Medina Group (Brett et al., 1990a, 1990b) indicate that many of the previous assumptions about the so-called "Thorold" are incorrect. First, although a 0.7 m to 3.0 m-thick greenish white mottled sandstone does occur over most of the area from Wayne to Oswego Counties westward into Niagara County, this is not all referable to the Thorold Sandstone. Indeed, the Thorold Sandstone occurs below the Clinton Group only at and near the type section near St. Catharine's, Ontario, and eastward to central Niagara County, New York (Figure 3). West of St. Catharine's, Ontario, "Lower Clinton Group" strata are completely removed by a later erosion surface. In the area west of Grimsby, Ontario, the Merrittton Limestone of the upper part of the Clinton Group rests with a sharp contact on light-colored beds that are actually layers of the upper Grimsby Sandstone (W.M. Duke, personal commun., 1989; Figure 3).

In the vicinity of the northern Niagara Gorge, a thin remnant of purple to greenish shale appears between the Thorold Sandstone and the phosphatic sandy carbonate horizon at the base of the Clinton Group. At one section just north of the Robert Moses Power Plant in the vicinity of Lewiston, New York, about 50 cm of this purple to greenish sandy shale is present below the base of the Neahga Shale (lowest Clinton Group unit). Fisher (1953a) recognized this interval in the northern Niagara Gorge and inferred that the green and purple shales should be included as a distinctive basal unit of the Neahga Shale. However, Fisher was apparently unaware that a sandy, brachiopod-bearing, phosphatic limestone or dolostone (Densmore Creek Bed, see below) occurs

at the top of the green and purple shales and separates these from the overlying dark grey, fissile, "true" Neahga Shale.

Another critical section is at Lockport Junction Road (New York Rte. 290) near the village of Hickory Corners. Fisher was aware of this outcrop and included this newly discovered section in an addendum in his 1953a paper. The full implications of this cut, however, were not realized until the 1980s, when a fresh exposure was made during road widening (see Brett et al., 1990a). This revealed an excellent section of typical Neahga Shale that has a sharp base at a distinct phosphatic pebble horizon that contains the brachiopod *Hyattidina congesta*. Fisher apparently saw the brachiopods, but he did not recognize that the phosphatic level here was correlative with the phosphatic bed (Densmore Creek Bed, herein) that he observed at Rochester. This phosphatic bed sharply separates the Neahga Shale from the underlying greenish shale with leperditian ostracodes. The latter shale has been termed the "Cambria Shale," with the Lockport Junction roadcut as the type section (Brett et al., 1990a, 1990b).

A distinctive unit lies approximately 1.75 m below the phosphatic marker bed at the base of the Neahga Shale at Lockport Junction Road. This unit forms a mottled pink and white ledge about 1.2 m thick that is composed of fine-grained, moderately well-sorted sandstone with abundant trace fossils (*Daedalus* and *Arthropycus*). These trace fossils are present in the Thorold Sandstone at Niagara Gorge and westward into Ontario. It is inferred herein that the pinkish sandstone bed 1.75 m below the phosphatic bed is, in fact, the Thorold Sandstone. A compa-

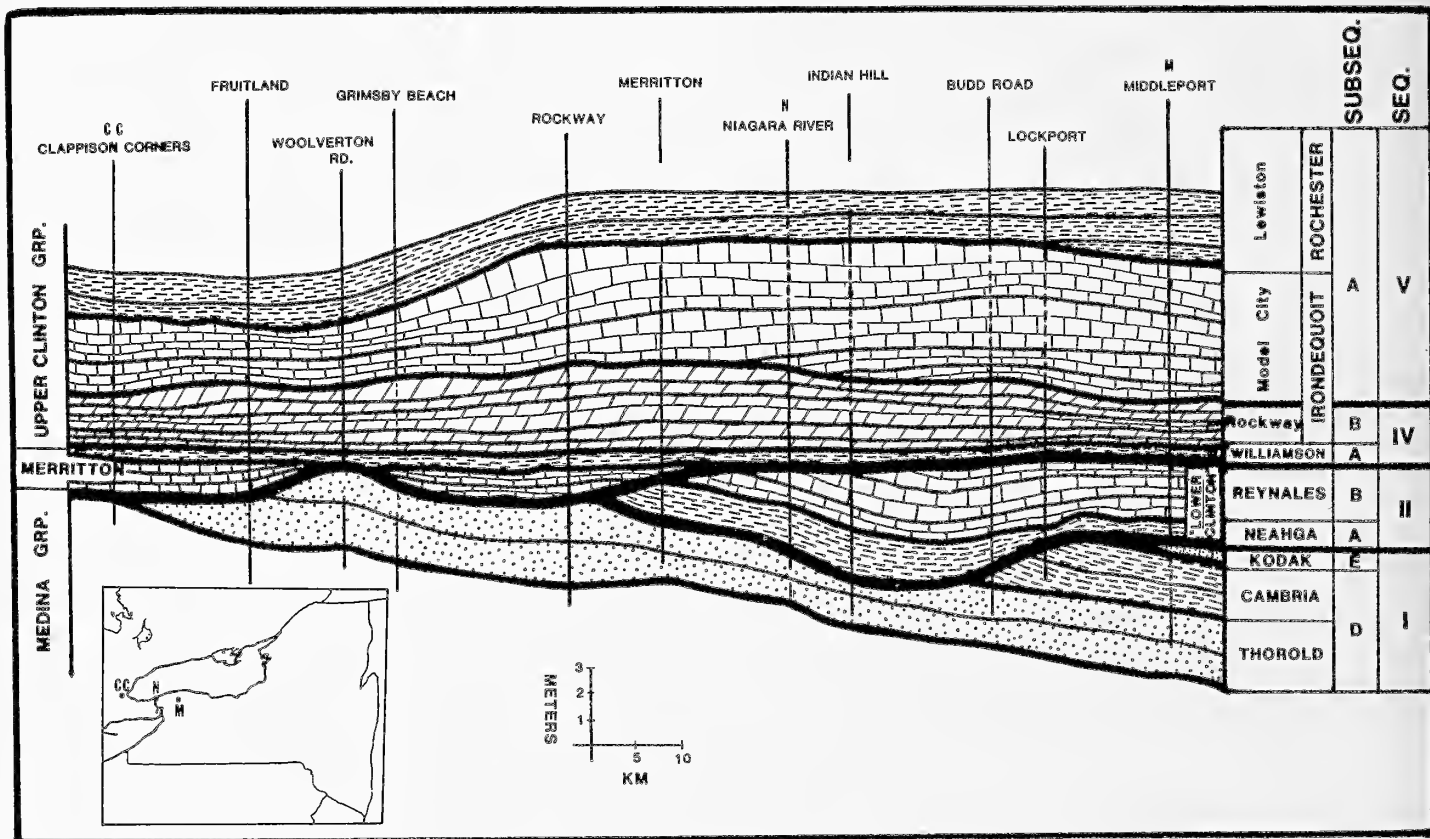


Figure 3. Regional cross-section of upper part of Medina Group (sequence I), lower part of Clinton Group (sequence II), and upper part of Clinton Group (Sequence IV and V) in western New York and southern Ontario (inset map gives location of sections). Note that the lower part of the Clinton Group (Neahga Shale through Reynales Limestone) is an unconformity-bounded sequence preserved as a wedge-like unit because of convergence of bounding unconformities near Merrittton, Ontario, where the Merrittton Limestone at the base of the Williamson Shale tongue rests on the Neahga Shale. Also, note the westward truncation of upper units of the Medina Group (Kodak, Cambria, Thorold) beneath the base of the Neahga Shale (black line denotes Densmore Creek Bed) (Modified from Kilgour, 1963).

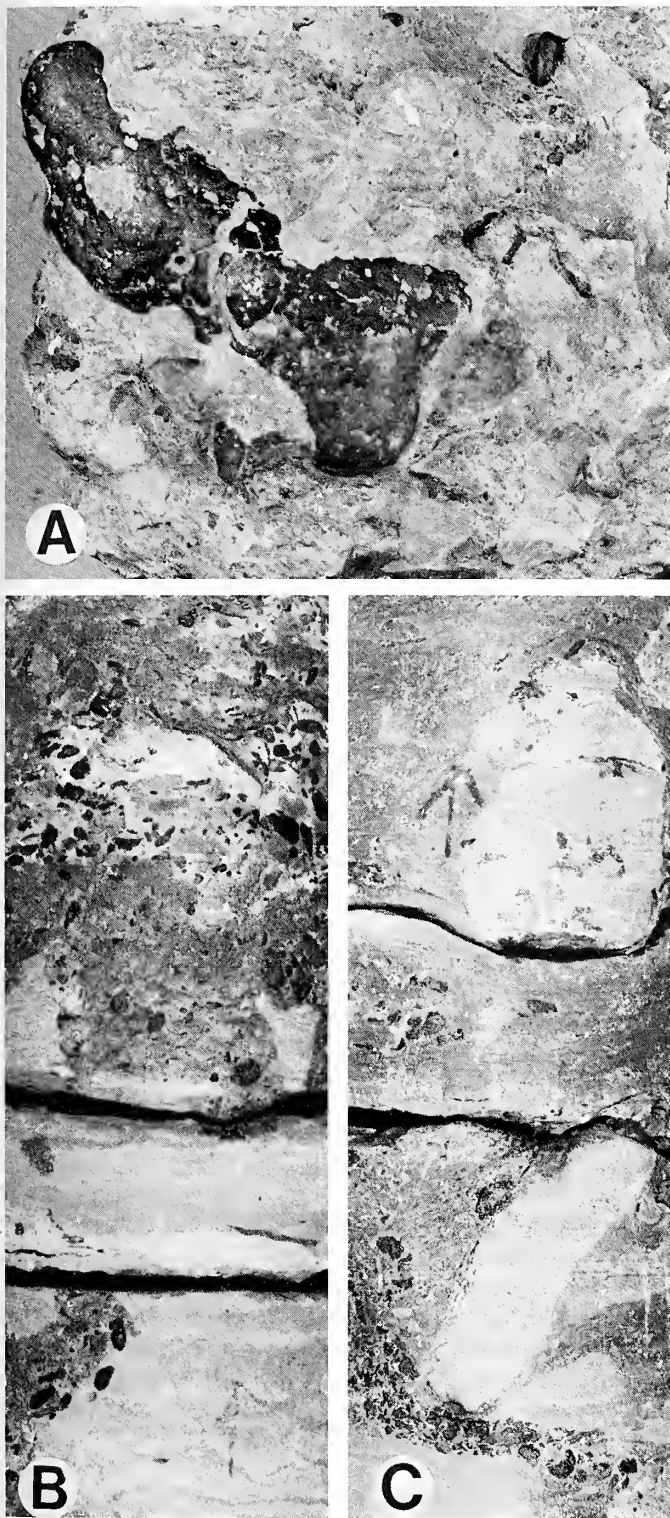


Figure 4. Densmore Creek Bed. A, Slab of lower part of Maplewood Shale with abundant bored black phosphatic clasts; Densmore Creek, Rochester, Monroe County, New York. B, Drill core through Clinton-Medina Group contact showing piping of phosphatic clasts of Densmore Creek Bed downward into Kodak Sandstone; Albion Landfill site, Albion, Orleans County, New York. C, Drill core through Clinton-Medina Group contact showing similar features; Rochester, Monroe County, New York.

able *Daedalus*-bearing interval has been traced eastward at least to Monroe County.

The 2.0 to 4.0 m-thick Cambria Shale occurs above the Thorold-equivalent interval with *Daedalus* at locations from eastern Niagara County and eastward past Rochester, New York. It underlies a greenish white bioturbated sandstone, referred to as the Kodak Sandstone, at Lockport and eastward.

Still higher green and purple shales occur above the 1.0 to 1.5 m-thick Kodak Sandstone in the Rochester area. Hence the sub-Clinton unconformity truncates, in westward order, first the post-Kodak shale, then the Kodak Sandstone, the Cambria Shale, and finally, in Ontario, the Thorold Sandstone (Figure 3). The strata beneath the Densmore Creek Bed therefore vary from place to place in a regular pattern.

An important observation made by Duke (1987) is that all units that underlie the Neahga-Maplewood Shales are typically light-colored, either white or pale greenish grey sandstone or green shale. These green or pale grey strata appear to grade downward through a transitional mottled zone into pinkish strata at most localities. Duke (1987) inferred that the light, non-red-colored interval underlying the Neahga-Maplewood Shales resulted from a secondary leaching of iron oxide, as reducing pore water derived from the dark green or black Clinton Group muds seeped downward into the older sands and muds. The appearance of a white "Thorold-Kodak" interval everywhere beneath the Clinton Group is therefore believed to be a diagenetic artifact rather than a depositional feature. The bases of the "true" Thorold Sandstone and the Kodak Sandstone are locally sharp, but these do not appear to be major beveling surfaces. Rather, they are simply minor (subsequence) boundaries (see Brett et al., 1990a, 1990b).

Fisher (1953a, p. 30) claimed, as did Gillette (1947), that the Thorold Sandstone was gradational into the overlying greenish grey Neahga and Maplewood Shales. He noted, for example, a gradual diminution of quartz content and increase in clay. However, Fisher evidently failed to recognize that these greenish "gradational" shales that locally overlie the Thorold Sandstone are set off from the "true" Neahga Shale by a major and regionally beveling unconformity. The supposedly gradational shales are indeed a part of the Medina Group and comprise different units in the Rochester area than in the Niagara area: post-Thorold shales (Cambria Shale) in Niagara County, and post-Kodak (i.e., younger) shales at Rochester. Hence the interval from above the Kodak Sandstone downward through the Thorold Sandstone (previously simply called "Thorold Formation") is herein removed from the Clinton Group and assigned to the Medina Group.

Neahga and Maplewood Shales

As currently defined, the basal formation of the Clinton Group is the Neahga Shale in western New York and adjacent Ontario, and the Maplewood Shale in the area of Monroe County, New York. The base of both units is drawn at a distinctive marker bed, herein termed the "Densmore Creek Bed". The top is marked by a second phosphatic bed, the "Budd Road Bed" (Figures 4-6; see below).

Densmore Creek Bed

A sandy phosphatic zone up to 15 cm thick with multigenerational calcareous sandstone clasts that contain small, phosphatic nodules is present above the Kodak Sandstone at Densmore Creek, 0.2 km east of Densmore Road, Irondequoit, New York (type section). It also occurs at the Genesee River Gorge, where it forms an excellent basal marker for

the Maplewood Shale (Figure 4A). Large, well-defined burrows pipe phosphatic clasts as much as 6.0-7.0 cm downward into the underlying greenish sandy shale that overlies the Kodak Sandstone (Figure 4B, C). These distinctive burrows characterize the basal surface of the bed at Densmore Creek and in some localities in the Niagara County region, and indicate relatively firm (probably overcompacted) but nonlithified sediments on the upper surface of the Medina Group at the time of deposition of the Neahga-Maplewood muds.

Phosphatic nodules and pebbles in the basal Densmore Creek Bed consist of glossy black collophane clasts (Boger and Sutphin, 1984). Small shells of high-spined gastropods and bellerophonitids occur abundantly as phosphatic steinkerns. West of the Rochester area, the phosphatic Densmore Creek Bed is readily recognizable to Niagara County, where it becomes a phosphatic sandy dolostone or limestone that ranges from 5 to 10 cm-thick and contains the brachiopod *Hyattidina*. A correlative 20 to 30 cm-thick sandy limestone with abundant brachiopods and bryozoans is present above the Thorold Sandstone at St. Catharine's, Ontario. East of the Rochester area, where the Maplewood Shale pinches out, the Densmore Creek Bed grades into the base of the Webster Bed (see below).

Neahga Shale

The Neahga Shale was referred to as the "lower Green Shale" by Hall (1843) and as the "Clinton Shale" by Grabau (1901), and erroneously as the Sodus Shale by Kindle and Taylor (1913) and the Furnaceville Shale by Chadwick (1918) and Williams (1919). Sanford (1935) named the Neahga Shale for its type section along the Niagara Gorge; he used the old Indian name ("Neahga") for the Niagara River. The Neahga Shale is platy, fissile, dark grey to olive greenish grey clay shale with minor amounts of quartz silt. The thickness varies from a feather-edge near Lockport and west of St. Catharine's, Ontario, up to about 2.0 m at the north end of the Niagara Gorge. The Neahga Shale is apparently truncated by a major late Llandoveryan unconformity at or near St. Catharine's, Ontario. The shale is absent along the Victoria Avenue roadcut in Jordan, Ontario. Although thin shales referred to as "Neahga" have been reported as far west as Grimsby, Ontario, these appear to be shales within the upper part of the Medina Group. Hence the distribution of the Neahga Shale is limited to the area between St. Catharine's and Lockport. At Lockport, New York, the Neahga Shale thins abruptly from about 1.5 m at the Lockport Junction roadcut to about 25 cm at the new Sommerset railroad cut (see Brett et al., 1990a, for details). It has been inferred, although not demonstrated, that the shale is absent east of Lockport (Fisher, 1953a). Drill cores taken by the U.S. Geological Survey from near the Niagara escarpment southward to Grand Island, New York (about 16 km to the northwest) also display thickness variations in the Neahga Shale. In northern cores, the Neahga Shale ranges up to about 2.0 m thick, as in the northern Niagara Gorge outcrops; however, the Neahga Shale beneath Grand Island is very thin (approximately 30 cm thick).

At all localities, the Neahga Shale bears a sparse *Eocoelia* brachiopod-dominated assemblage. Fisher (1953a, p. 34) provided a faunal list of twenty-three species of brachiopods, bivalves, gastropods, nautiloids, and ostracodes from the Neahga Shale. Gillette (1947, p. 23) reported the zonally diagnostic ostracode *Zygobolba excavata* from the Neahga Shale in Niagara County. Both Gillette (1947) and Fisher (1953a) recognized *Z. curta*, also suggestive of the *Zygobolba excavata* Zone, from Niagara Gorge. Rexroad and Rickard (1965, p. 1219) recorded conodonts of the *Neospathognathodus celloni* Zone (Zone II) from the Neahga Shale at Niagara Gorge. Nicoll and Rexroad (1969) subse-



Figure 5. Bored platter-like clasts of phosphatic sandy limestone from base of Neahga Shale. Merriton railroad cut near Thorold, Ontario.

quently reassigned the Neahga to the *Icriodina irregularis* Zone (or Zone I). Recently, M. Kleffner (personal commun., 1989) obtained conodonts diagnostic of the *Distamodus kentuckiensis* (*Icriodella discreta/deflecta*) Zone; this indicates the Neahga Shale is of Aeronian age. Gillette (1947) noted the presence of *Eocoelia hemispherica* and *E. plicatula* in the Neahga Shale in Niagara County, although he admitted that poor preservation prevented precise species identification. The presence of *E. hemispherica* suggests that the Neahga Shale belongs to the lowest portion of Ziegler's (1966) evolutionary zonation for *Eocoelia*. Together, these lines of evidence indicate a Llandoveryan B-2 to C-1 age assignment for the Neahga Shale. This age is corroborated by the discovery of the brachiopod *Hyattidina congesta* at the base of the Neahga Shale at Lockport, (see Fisher, 1953a, p. 35), and subsequently at the Niagara Gorge and St. Catharine's, Ontario.

In terms of lithology, the Neahga Shale is essentially undifferentiated platy green to grey shale, with the thin (1-3 cm-thick), phosphatic, calcareous sandstone of the Densmore Creek Bed everywhere at its base. Fisher (1953a, p. 36) correctly recognized a disconformity between this bed and the underlying sandy green shales with leperditian ostracodes (Cambria Shale of the uppermost Medina Group, herein) at Lockport Junction Road. A thin, bioturbated, brachiopod-bearing sandstone (Densmore Creek Bed, herein) at Niagara Gorge separates the "true" Neahga Shale from 20 to 25 cm of green and purplish shales that overlie the Thorold Sandstone; these shales also apparently belong to the Cambria Shale. The Densmore Creek Bed is present in all sections, and is more or less rich in black phosphatic nodules at various loca-

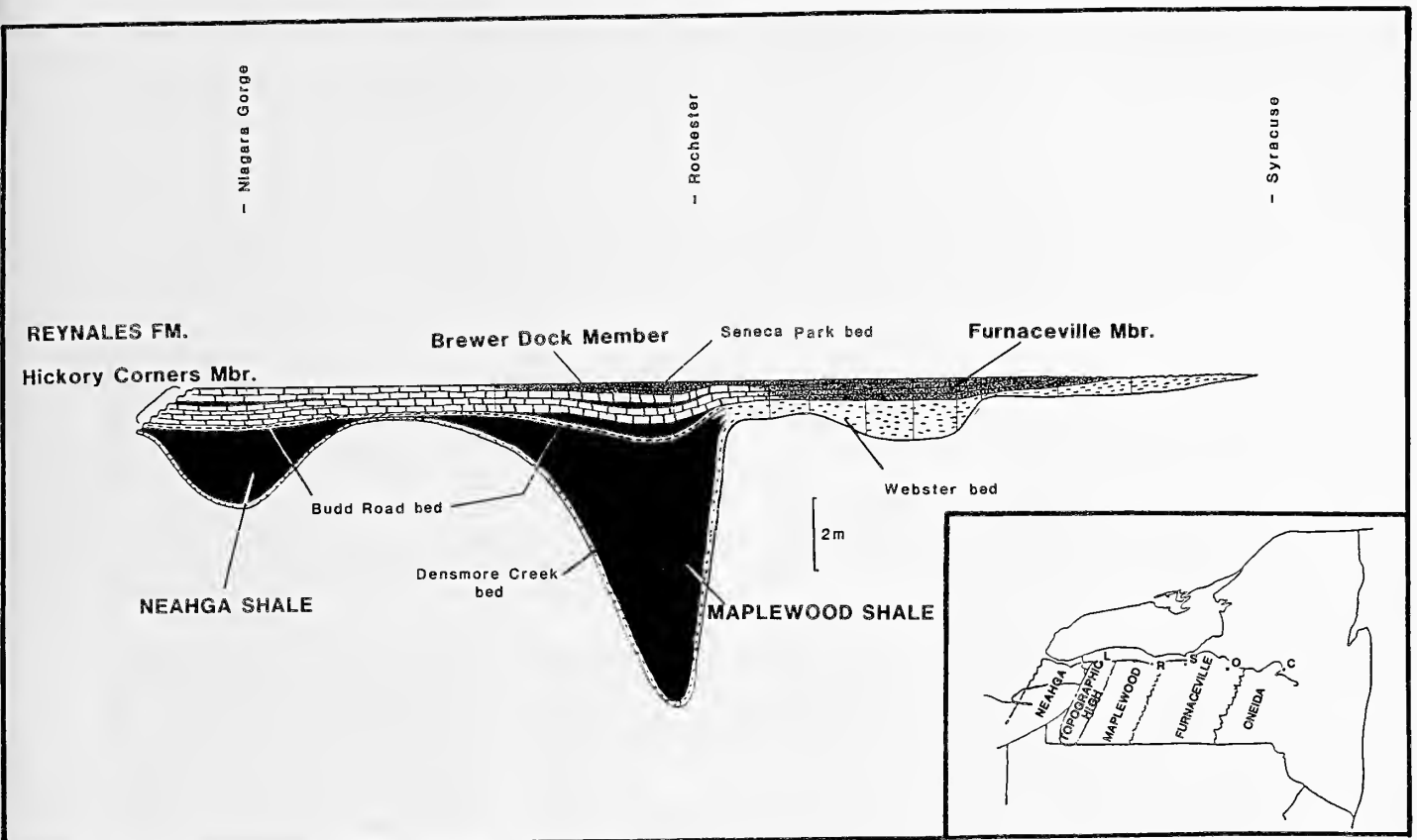


Figure 6. Regional cross-section of the lower part of the Clinton Group between Syracuse, New York, and St. Catharine's, Ontario. Note the presence of two minor depocenters (for Neahga and Maplewood Shales, respectively) separated by a minor arch. Also, note eastward passage of Maplewood Shale into a highly condensed, multigenerational phosphatic conglomerate (Webster Bed). West of Niagara Gorge the Neahga Shale is truncated by the major mid-Clinton Group angular unconformity.

tions. This basal bed is particularly well-developed at the Merritton railroad cut at Thorold, Ontario, where a 15-20 cm-thick, highly fossiliferous, sandy, phosphatic limestone is amalgamated to the top of the Thorold Sandstone. The sand grains within this unit have been reworked from the underlying Thorold Sandstone. Thus although the contact is probably disconformable, it may appear gradational locally due to reworking of the older sands into the younger calcareous, muddy sediments. The base of the Neahga Shale at this locality contains large (up to 20 cm long), flat (up to 1.0 cm thick), black-stained and intensely *Trypanites*-bored clasts of the underlying phosphatic sandy limestone (Figure 5). Multigenerational phosphatic limestone clasts with obvious hardground features are very similar to clasts seen in the basal Maplewood Shale and below the base of the Furnaceville Member eastward in Monroe County. Indeed, the phosphatic calcareous sandstone or sandy limestone unit at the base of the Neahga Shale is correlative with the Densmore Creek Bed of Monroe County.

Maplewood Shale

The Maplewood Shale was named by Chadwick (1918, p. 346) for 6.0 to 7.0 m of distinctly greenish grey, platy, chlorite-rich shale at the Genesee River Gorge in Rochester, Monroe County. It has been referred to earlier as "Sodus Shale" by Hartnagel (1907) and "Lower Green Shale" by Hall (1843). As does the Neahga, the Maplewood shows a substantial variation in thickness, and thins both east and west of the type section. It had previously been recorded only from sections

east of the Genesee Gorge, where it thins to 5.3 m at Densmore Creek on the west side of Irondequoit Bay and to 5.0 m at Glen Edith 3.2 km to the east of Irondequoit Bay. As noted by Fisher (1953a), the latter is the most easterly outcrop of the Maplewood Shale. New excavations on the property of the Xerox Corporation in the town of Webster, 10 km northeast of Glen Edith, indicate the absence of Maplewood Shale at this location. Hence the Maplewood Shale pinches out rapidly north-eastward, from nearly 7.0 m to a feather-edge within about 10 km (see below).

West of the Genesee River Gorge, there are no outcrops of the Maplewood Shale, with the exception of 0.6 m of green phosphatic shale along Oak Orchard Creek in the town of Medina. However, a drill core from a landfill site at Albion, Orleans County, New York, shows about 60 cm of dark greenish grey shale. This shale is somewhat intermediate in lithology between typical Neahga and Maplewood Shales, and is bounded at its base by a distinctive 10 cm-thick sandy zone packed with black phosphatic nodules, some of which occur in larger clasts of calcareous sandstone (Figure 4B). Large burrows pipe phosphatic material up to 6 cm into the underlying bioturbated green sandstone of the presumed Kodak Formation (Figure 4B).

The Maplewood Shale has an even sparser fossil assemblage than the correlative Neahga Shale in the west. Although Fisher (1953a, p. 34) reported twenty species, most of these were represented by fewer than five specimens and were confined to the basal Densmore Creek Bed. Poorly preserved specimens of *Eocoelia* sp. are relatively common

in most of the shale. Recent excavations for the Driving Park Bridge in the Genesee Gorge yielded large blocks of Maplewood Shale, which were split and carefully examined. S.J. Cieurca (personal commun., 1988) obtained several new fossils from this exposure; these include possible phyllocarids, complete camerate crinoids (apparently a new species of a dimerocrinitid), nautiloids, linguloids, acritarchs, and paly-nomorphs. Fisher (1953b) reported a diverse assemblage of seventeen species of acritarchs now assigned to the genera *Leiosphaera*, *Verhachium*, and *Micrhystidium* (M. Miller, personal commun., 1985). No zonally significant ostracodes or conodonts have been obtained from the Maplewood Shale, in contrast to the Neagha, but its physical continuity with the latter formation indicates that it is of the same age. Berry and Boucot (1970) tentatively assigned a Llandoveryan C-4 age to the Maplewood Shale. This assignment is very doubtful, and in all probability the unit is of Llandoveryan B-2 to C-1 age.

Similar to the Neagha Shale, the Maplewood Shale is not lithologically divisible, except for the 5-20 cm-thick phosphatic Densmore Creek Bed at its base. Very thin stringers of phosphatic granules have been found at scattered levels within the Maplewood at the Rochester Gorge, but these are difficult to recognize and do not appear to be trace-

able. The upper meter of the Maplewood has very thin (<1.0 cm), laminated, calcareous siltstone beds with sharp, slightly grooved soles. Otherwise, there are no interbeds of any sort within the shale. The upper boundary of the unit is drawn at the base of a thin (1-2 cm thick) but distinctive phosphate-rich, calcareous siltstone with *Eocoelia* and rare *Hyattidina* shells. This unit, which is designated the "Budd Road Bed" (see below), marks the base of the Reynales Limestone. This bed is traceable laterally from Monroe County at least to the Niagara Gorge, and therefore marks the top of both the Maplewood and Neagha Shales.

On the basis of physical stratigraphy, the Maplewood and Neagha Shales are laterally equivalent formations (Figure 6). They are also coeval, as indicated by identical acritarch assemblages. The units are bounded at the base by the Densmore Creek Bed, and at the top by the Budd Road Bed of the Reynales Limestone (Figure 6). Fisher (1953a) considered the Neagha and Maplewood Shales to be nearly identical facies of slightly different age. He believed the Maplewood Shale was younger than the Neagha Shale, because he correlated the Densmore Creek Bed at the base of the Maplewood Shale with the Budd Road Bed that occurs at the top of the Neagha Shale. He evidently did not recognize that the Densmore Creek Bed could be traced continuously at

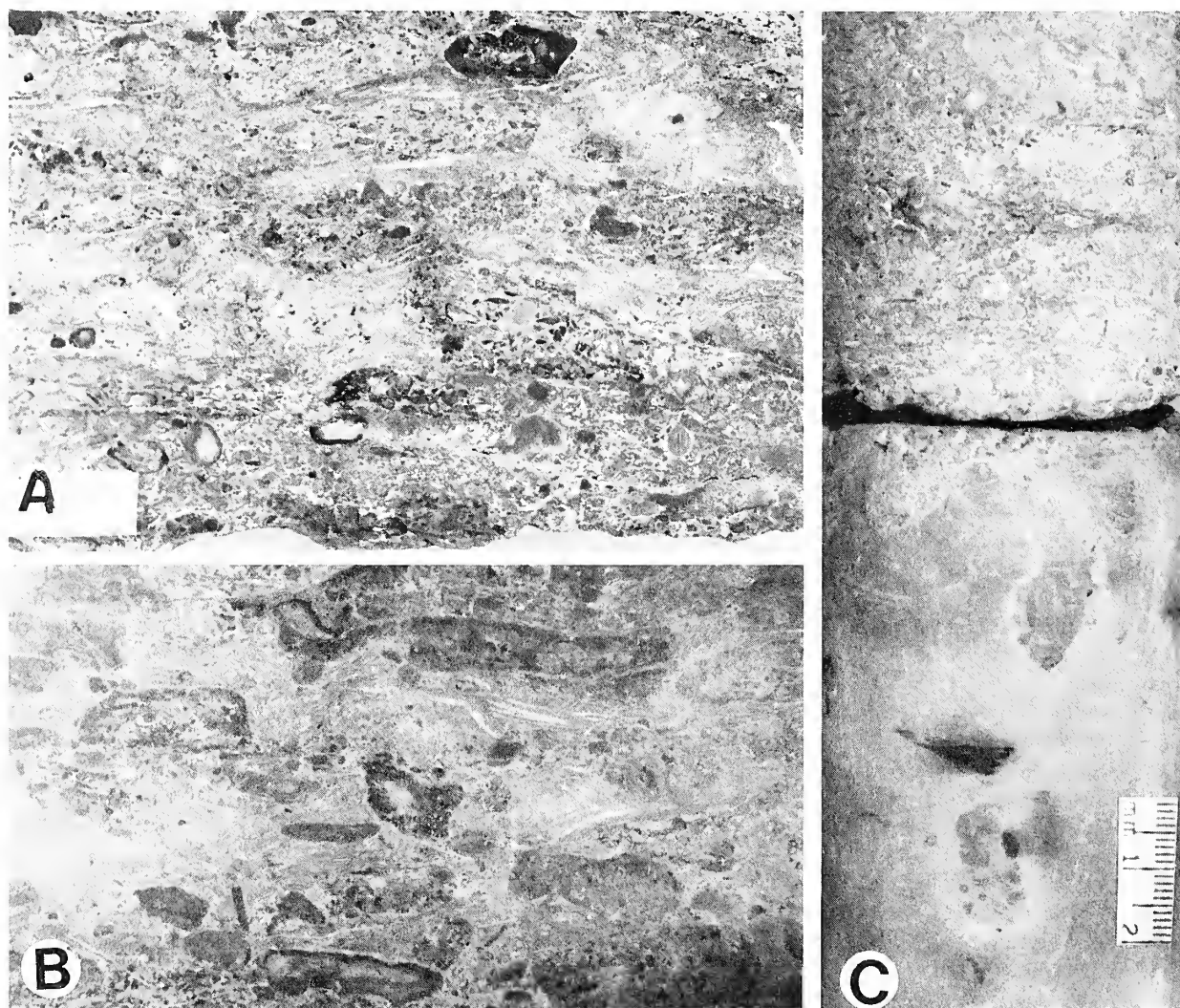


Figure 7. Webster Bed. A, Drill core through basal contact of Webster Bed; note piping of phosphatic material downward into underlying Kodak Sandstone. B, C, Polished slabs of Webster Bed showing flat, phosphatic, sandy limestone clasts with smaller phosphatic clasts within (multigenerational clasts); block from Xerox Corporation property, Webster, Monroe County, New York.

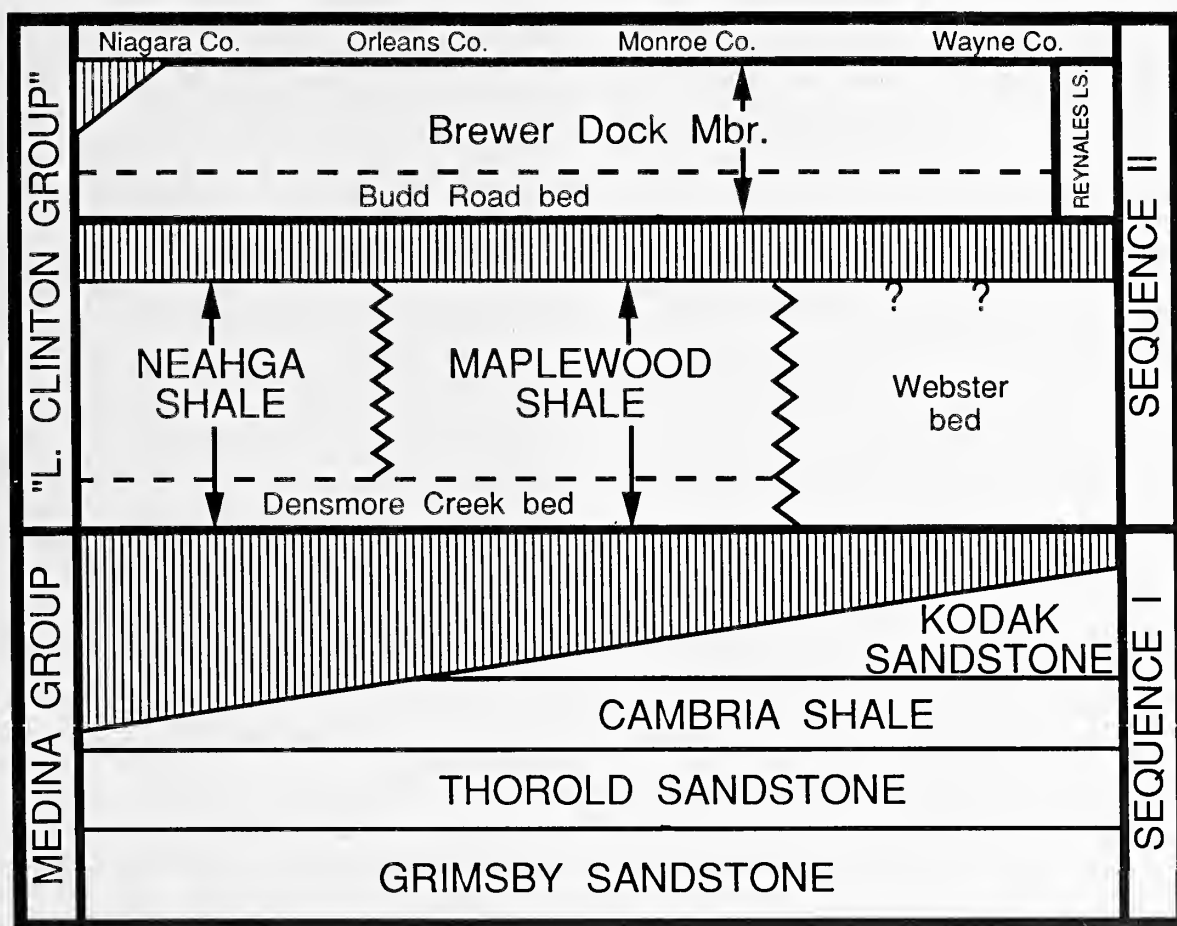


Figure 8. Summary chart of chronostratigraphic relationships of Maplewood-Neahga Shales and boundary phosphatic beds. Note that east of Rochester, New York, the Maplewood Shale interval is represented by a thin (10 to 20 cm) hematitic, phosphatic, limestone conglomerate, the Webster Bed.

the base of the Neahga and Maplewood Shales from Monroe County westward into Ontario. Therefore, he correlated the Maplewood Shale with a portion of the Reynales Limestone in western New York. As indicated below, however, the Reynales Limestone has a distinctive, regionally traceable internal stratigraphy that indicates that the limestones of the Hickory Corners Member of western New York are precisely equivalent to the lower part of the Reynales Limestone in the Monroe County area.

The Neahga and Maplewood Shales are thus time-correlative and extremely similar lithologically. Both are composed of clay shale with an average clay content of 93%, and only minor calcite and quartz. Consequently, the terms "Neahga" and "Maplewood" are essentially synonymous local names for one and the same regionally extensive unit in western New York State and adjacent Ontario, and presumably the subsurface of northwestern Pennsylvania and northeastern Ohio. The term "Maplewood" could probably be applied uniformly to this unit, as was proposed by Chadwick (1918) long before Sanford (1935) proposed the name "Neahga." However, there are very subtle facies differences that could warrant maintaining the separate names. The Maplewood Shale is typically a brighter green-colored shale, whereas the Neahga Shale has a darker grey coloration. The Neahga is also somewhat more fossiliferous, and contains a slightly more diverse fauna than the Maplewood.

Presumably, the Maplewood Shale at Rochester is a more proximal

mud facies. The fact that the Maplewood Shale pinches out completely within a short distance to the east of Rochester suggests that a basin margin hinge existed in the area of eastern Monroe County during deposition of the lowest Clinton Group.

No sections have been observed between Monroe County and St. Catharines, Ontario, in which either the green or dark grey facies are absent. There is a region, centered on Lockport, New York, in which the shale pinches to a feather-edge (5-20 cm). However, despite the thinness of the Neahga Shale at this locality, both the basal Densmore Creek Bed and overlying Budd Road Bed remain distinct and nearly identical in appearance to all other locations. This area of minimum thickness of the Maplewood Shale can be traced in the subsurface to the southwest. Overall, the evidence suggests that there were two weakly differentiated depocenters for the greenish Maplewood Shale and grey Neahga Shale. These two shales are separated by a southwest-trending topographic high, centered at Lockport, New York, that nearly divided the basin during deposition of these muds. This topographic high is oriented approximately along the same strike as the basin hinge, which trends southwestward from immediately east of Rochester to eastern Allegheny County (subsurface data from Van Tyne, 1966).

Webster Bed

As noted above, the Maplewood Shale pinches out abruptly near Webster, New York, in northeastern Monroe County. Drill cores from

the Xerox Corporation property at Webster display a 30 cm-thick, red, hematitic, multigenerational phosphatic conglomerate bed interposed between the overlying Reynales Limestone and underlying greenish grey sandstone and mudstone that probably belongs to the Kodak Sandstone or Cambria Shale. Fisher (1953a, p. 31) recorded a thin zone of "phosphate pellets" along the contact between the "Thorold" (=Kodak Sandstone) and the "Furnaceville Iron Ore" along Fish Creek at Wheatland. A similar observation was made by Gillette (1947) at the base of the Fruitland Iron Ore pit at Ontario Center (type section of the Furnaceville). About 45 km to the east of the Genesee River at Salmon Creek, in the town of Wallington, Wayne County, New York, a phosphatic conglomerate intervenes between a few centimeters of green shale, with phosphate pebbles at the base of the Furnaceville Member and the underlying Kodak Sandstone. Fisher's (1953a) conclusion that this phosphatic multigenerational conglomerate is the local, highly attenuated equivalent of the Maplewood Shale is concurred with in this report. This unit is termed the "Webster Bed" herein, for exposures and drill cores taken on the property of the Xerox Corporation near Salt Road in the town of Webster, Monroe County, New York.

The Webster Bed is a thin (10-20 cm) unit of bluish grey to red, hematitic, phosphatic limestone clasts that is laterally equivalent to the Maplewood Shale (Figures 6-8). The base of this bed bears precisely the same depositional relationship to the underlying Kodak Sandstone as does the Densmore Creek Bed to the west (Figure 6). Phosphatic nodules are piped downward 5-10 cm into the underlying bioturbated sediment, which is leached and greenish in color (Figure 7). The Webster Bed is somewhat thicker and more complex lithologically than the Densmore Creek Bed, however. Its top typically contains hematitic ooids and some hematitized clasts and fossil fragments. Particularly noteworthy of this unit are multigenerational clasts of phosphatic limestone (Figure 7). These clasts, which may be up to 10.0 cm across and up to 2.0 cm thick, are sandy limestone with dark rinds and include smaller phosphatic nodules and granules internally. Some of the phosphatic pebbles within the larger clasts have even smaller phosphate grains within them (LoDuca, 1988). Hence in some cases, at least three generations of phosphatization are represented. This strongly suggests that the Webster Bed represents a considerable time interval, and probably is laterally equivalent to the entire 6.0-7.0 m thickness of the Maplewood Shale, including the Densmore Creek Bed a short distance to the west.

At Webster, New York, the Webster Bed directly underlies a limestone assignable to the Wallington Member of the Reynales Limestone. Twenty kilometers farther east in the area of Salmon Creek, Wallington Township, Wayne County, the 10-20 cm-thick phosphatic conglomerate layer occurs either below or as the basal unit of a fossil fragmental and oolitic hematite referred to herein as the "Furnaceville Member." This relationship appears to exist eastward at least to the area of Bear Creek, where the Reynales Limestone changes into the Bear Creek Shale facies (see below). An oolitic hematite, still referable to the Furnaceville Member, underlies the lateral equivalent of the Wallington Member (i.e., Bear Creek Shale) in this area, and a phosphatic conglomerate bed (Webster Bed?) that is a few centimeters thick occurs between this unit and the underlying sandstone. Farther east, at Martville, Cayuga County, New York, Gillette (1947, p. 161) recorded a white conglomeratic sandstone beneath the Furnaceville Member with a layer of quartz pebbles and phosphatic nodules approximately 0.6 m below the contact. This unit may represent the eastward extension of the Webster Bed. At this location, it would appear that the Webster Bed grades laterally into a quartzose conglomeratic sandstone, the Oneida

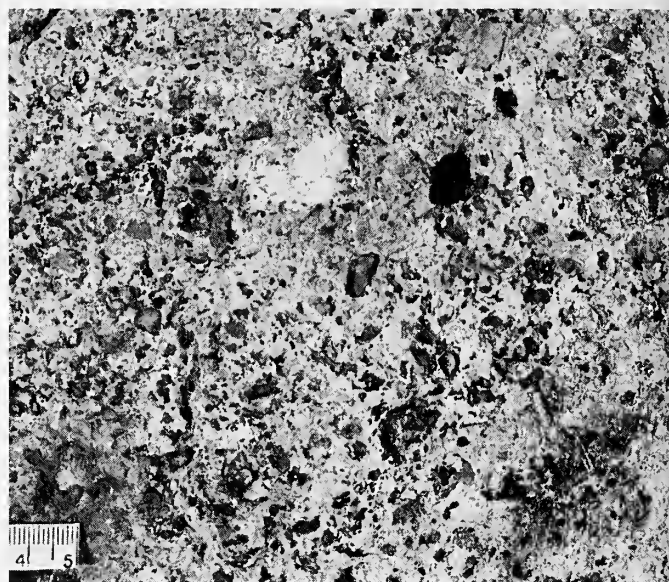


Figure 9. Budd Road Bed of the Reynales Formation. Slab shows closely packed black phosphatic nodules, fossil steinkerns, and bored limestone clasts; Lockport Junction roadcut, Cambria, Niagara County, New York.

Conglomerate, which rests unconformably above the Medina Group farther to the east.

Correlation with equivalent facies

It is possible to trace facies within the Webster-Maplewood interval westward from conglomeratic strandline deposits in Oswego County (Oneida Conglomerate) into a compact, multigenerational phosphatic conglomerate (Webster Bed) that may represent a very shallow, sediment-bypassed environment. Still farther west, an abrupt increase in rate of subsidence has produced a minor trough that has collected fine muds and minor silts (Maplewood Shale) that bypass the eastern gravelly shelf area and accumulate in a relatively quiet, albeit nearshore, shallow-water environment. The presence of pyrite and phosphate likely indicates reducing conditions on or within the seafloor in this area. Highly reducing conditions may have severely restricted the benthic fauna. Westward, this shale unit nearly pinches out on the Lockport high, but an equivalent, slightly darker grey and more fossiliferous shale (Neahga Shale) thickens westward to the Niagara region. A thin limestone bed is present above the Densmore Creek Bed immediately east of the Niagara region. This indicates that the Neahga Shale may pass westward into an argillaceous to arenaceous, fossil-rich carbonate facies.

The Neahga Shale and age-equivalent strata are absent in a broad region from St. Catharine's northwestward to Owen Sound near the southernmost part of the Bruce Peninsula in Ontario (Figure 2). At Owen Sound, a distinct unit, the Dyer Bay Limestone, occurs above the Medina Group-equivalent Cabot Head Shale. Although the Dyer Bay Limestone is poorly dated at present, limited biostratigraphic evidence, based on the occurrence of *Zygobolba williamsi* in the upper portion of the formation and the presence of the brachiopod *Virgiana* in the lower part of the Dyer Bay Limestone, indicates a Llandoveryan B-3 to early C-1 age for this unit. Hence it is the approximate age-equivalent of the Neahga Shale, and perhaps the immediately overlying lower part of the Reynales Limestone. Furthermore, the presence of abundant multigenerational phosphatic clasts near the base of the Dyer Bay Limestone

strongly suggests a physical correlation with the basal phosphatic, calcareous unit (Densmore Creek Bed) of the Neahga-Maplewood Shale interval. The Dyer Bay Limestone may represent a lateral equivalent of the Neahga Shale and lower part of the Reynales Limestone that is preserved on the northwestward side of the Algonquin Arch. This region of truncation of "Lower Clinton Group" units between St. Catharine's and Owen Sound presumably coincides with the main axis of the Algonquin Arch. It is interesting that the axis of this arch probably trended north-east-southwest and therefore was subparallel to the minor Lockport high (noted above). Both could be interpreted as units that reflect minor forebulge arching that locally subdivided the Maplewood-Neahga Shale basins.

Reynales Limestone

The Reynales Limestone is a rather heterolithic unit of interbedded brachiopod- and crinoid-rich grain- and packstones, argillaceous and pelletal wacke- and packstones (calcsiltites), nodular wackestones, and greenish to grey shales. Paxson (1985) provided detailed descriptions and interpretations of the petrography of this unit. Originally named the "Pentamerus limestone" by Hall (1843) in recognition of the abundance of *Pentamerus oblongus* at Rochester, the unit was mistakenly correlated with the Wolcott Limestone by Hartnagel (1907). The Wolcott is a stratigraphically higher *Pentamerus*-bearing limestone in central New York.

The age of the Reynales Limestone is debatable. The entire unit (Brewer Dock-Wallington Members) apparently belongs to a single ostracode zone (*Zygobolba excavata* Zone) that can be correlated with a relatively thin interval of the lower part of the Rose Hill Shale in Pennsylvania (Ulrich and Bassler, 1923; Gillette, 1947). Nicoll and Rexroad (1969) assigned the Reynales to the *Neospathognathodus celoni* Zone on the basis of conodonts. These conodonts suggest a late Aeronian age. However, Rickard (1975) assigned the Reynales Limestone to the Llandoveryan C-2 based on the presence of *Eocoelia intermedia*.

Recent conodont work by M. Kleffner (personal commun., 1990) suggests a possible unconformity near the base of the Reynales. Conodonts indicate that the lowest beds of the Reynales Limestone and the underlying Neahga-Maplewood Shales may be of Llandoveryan C-2 age, whereas the overlying Reynales Limestone is of late C-4 to C-5 age. These results are tentative and are not reflected in the correlation charts of this report (Figures 3, 8). The major unconformity, if there is one, may be suggested to lie actually below the Budd Road Bed at the contact between the Reynales Limestone and the underlying Maplewood-Neahga Shales. Conodonts obtained from phosphatic limestones a few centimeters above this contact may well be reworked from the underlying shales. At present, it can be noted that age relationships are only incompletely understood, and require further study.

Western facies: Hickory Corners Member

Chadwick (1918, p. 344-345), who formally named the Reynales

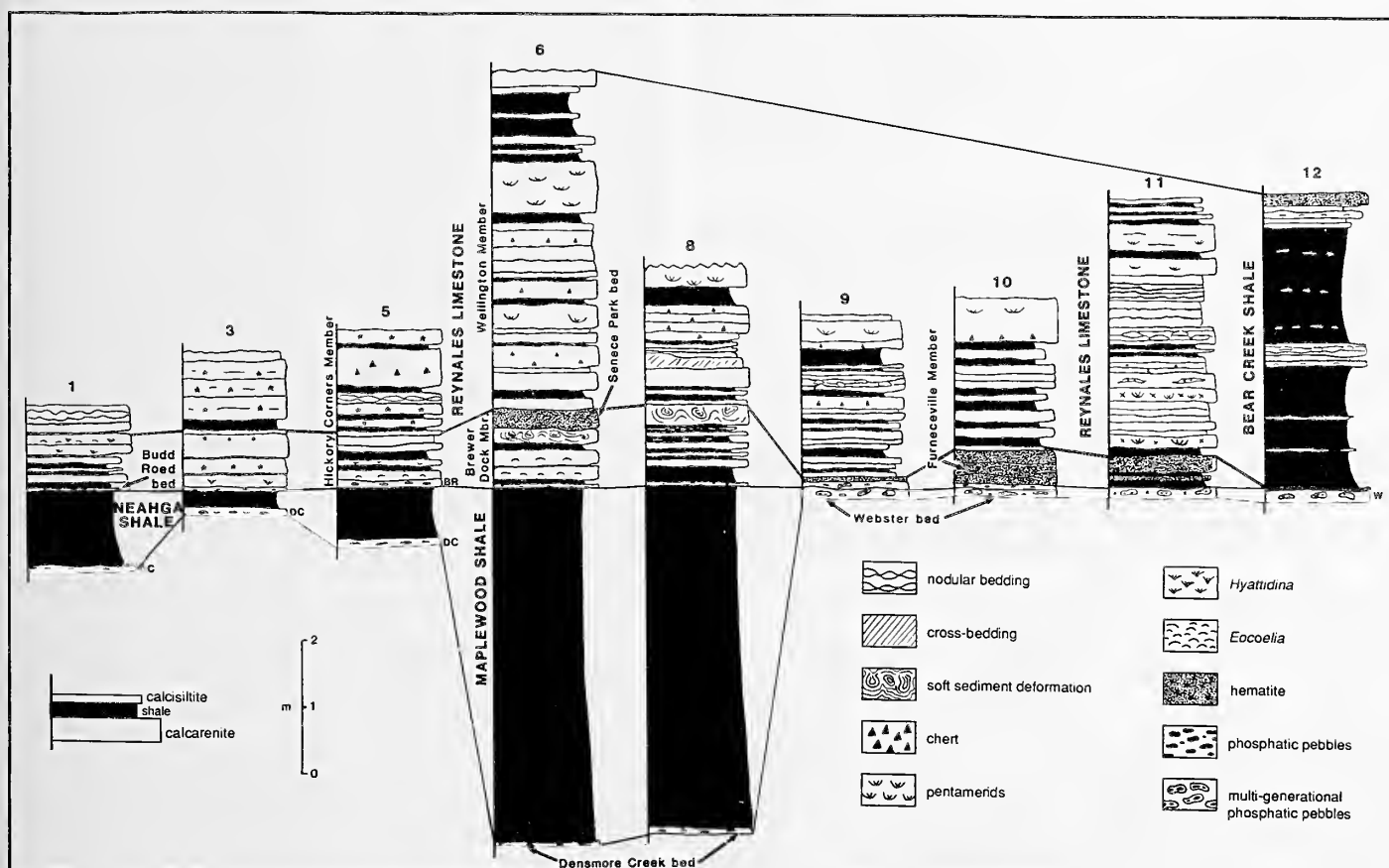
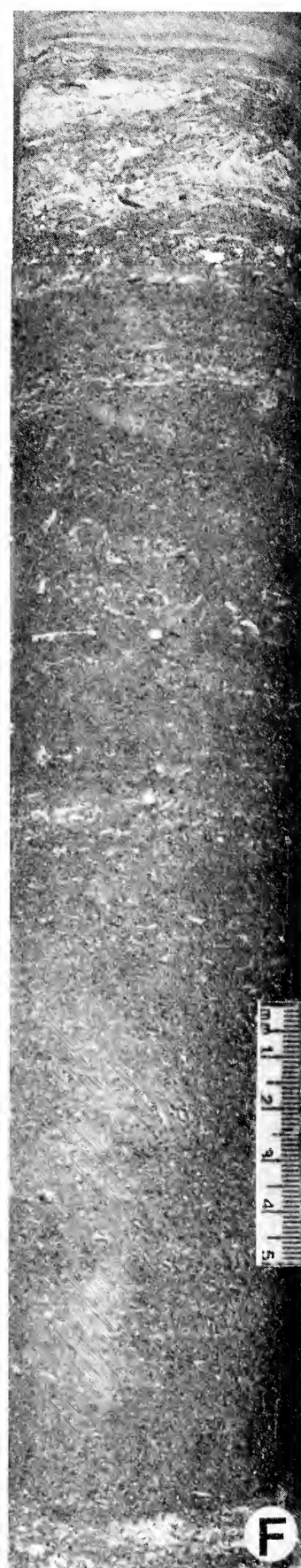
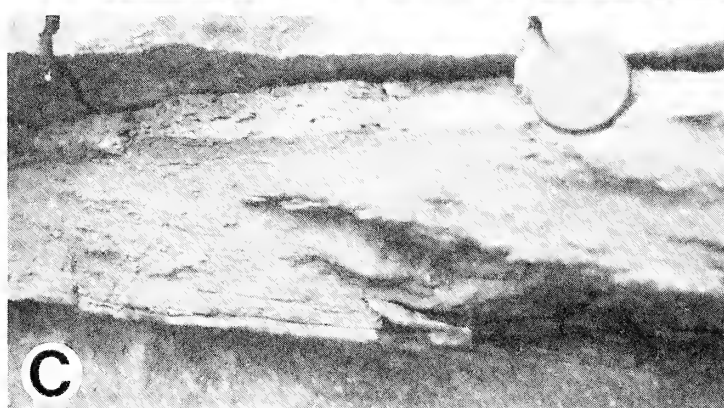
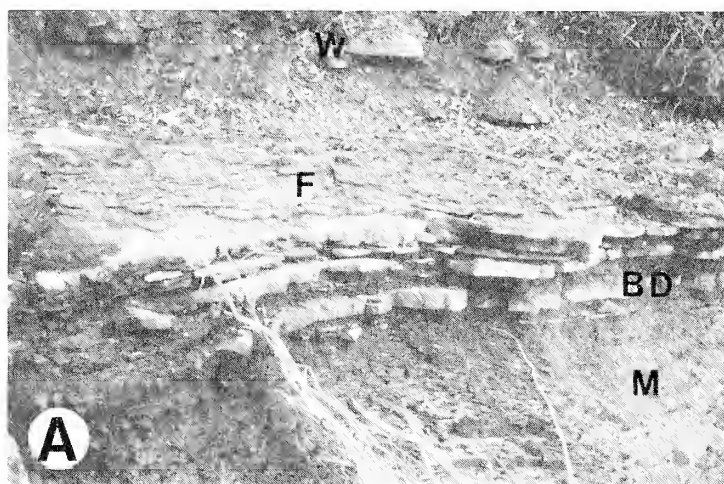


Figure 10. Fence diagram illustrating microstratigraphic relationships of "Lower Clinton Group" (Neahga-Maplewood and Reynales) strata in Ontario and western New York State. Locations of measured sections are shown in Figure 1.



Limestone, chose a rather atypical exposure at Reynale's Basin near Middleport, Niagara County, as the type section. In this area, the Reynales Limestone consists of about 2.5 m of interbedded, medium bluish grey to dark grey, buff-weathering, silty, dolomitic limestone. Much of this is a brachiopod- and crinoid-rich packstone with thin shale interbeds. Small chert nodules occur in a few beds near the top (see Paxson, 1985). This more or less undifferentiated interval is characterized by the brachiopods *Hyattidina congesta*, *Platystrophia*, *Dalejina*, *Coolinia*, and *Eocoelia*; small rugose corals (*Enterolasma*); and the trilobites *Encrinurus*, *Calymene*, and *Bumastus* (Figures 9-14). Eckert (1989) recently described a new echinoderm fauna from the Reynales Limestone of Niagara County. This consists of a species of disparid inadunate crinoid with pentalobate columns, a calceocrinid, a myelodactylid, two camerates, and two flexible crinoids; all represent new species. Pentamerid brachiopods do not occur in any sections in Niagara County or Ontario.

The Reynales Limestone at the type section is equivalent and essentially identical to the Hickory Corners Member. The latter unit was proposed by Kilgour (1963) for the thin-bedded, argillaceous, crinoidal pack- and grainstones characterized by *Hyattidina* at the Lockport Junction roadcut near the hamlet of Hickory Corners, Niagara County, New York. Kilgour (1963) recognized that Chadwick (1918) and others had incorrectly included 1.2 to 2.5 m of medium to dark grey fine-grained dolostone with rare fossils in the Reynales Limestone at its type section and elsewhere. This unit, which Kilgour (1963) assigned to the Rockway Member of the Irondequoit Formation, is separated from the "true" Reynales by a major sequence-bounding unconformity which, as noted, bevels the "Lower Clinton Group," including the Reynales Limestone, to the west (Figure 3). In contrast, the overlying dark grey dolostone beds of the Rockway Member extend from central New York into Ontario (Lin and Brett, 1988). A distinctive phosphatic bed, the Second Creek Bed (see Lin and Brett, 1988), lies between the Rockway Member and the beveled upper surface of the "true" Reynales Limestone.

The term "Hickory Corners Member" is probably unnecessary, because it is a synonym of an earlier-named unit. The "Hickory Corners Member" is only the western extension of both the Brewer Dock Member and the lower beds of the Wallington Member of the Reynales Limestone (see below).

Eastern facies: Brewer Dock, Furnaceville, and Wallington Members

The type Reynales Limestone of Niagara County is quite unlike the "classic" pentamerid facies characteristic of the Genesee Gorge region and elsewhere east of Monroe County. At the Genesee Gorge in Rochester, the Reynales Limestone is about 6.5 m thick and is differentiable into three units. These are, in ascending order, the Brewer Dock Member, the Seneca Park Bed (new designation), and the Wallington Member.

Budd Road Bed.—The base of the Reynales Limestone is drawn to the lower boundary of a unit termed herein the "Budd Road Bed," a 1.0 to 6.0 cm-thick silty limestone with very small phosphatic nodules and granules (Figure 9). This unit is traceable at least from Monroe County (Glen Edith) westward to the Niagara Gorge; it is present in all outcrops and drill cores in this region, but is best-developed in the area of Lockport. The unit is named for exposures at Budd Road near the hamlet of Hickory Corners, Niagara County, New York.

Brewer Dock Member.—The Brewer Dock Member was named for Brewer's Dock on the Genesee River at the lower falls in Rochester Gorge, Monroe County, New York (Sanford, 1935). The Brewer Dock Member is approximately 0.5 to 1.0 m thick and consists of light grey crinoidal- and bryozoan-rich limestone with considerable shale near the base (see Paxson, 1985, for details of petrology; and Figures 10 and 11 herein). The base of the Brewer Dock Member is drawn at the lower boundary of the Budd Road Bed.

It should be noted that recent conodont sampling of the Reynales Limestone has revealed an abrupt change in conodont assemblages within the Brewer Dock Member (Kleffner, 1990, personal commun.). A diverse assemblage, typical of the *Distamodus kentuckiensis* Zone (\approx *Icriodella discreta*–*Icriodella deflecta* Zone) occurs in the lower phosphatic limestone beds of the Brewer Dock Member. This assemblage is identical to that of the underlying Neagha–Maplewood Shale interval and suggests an early Aeronian age (Llandoveryan B to C-2). A major change in the conodont fauna apparently coincides with the base of the Seneca Park Bed. This faunal change also occurs near the base of the apparently equivalent non-hematitic grainstone bed to the west. Conodonts from the Seneca Park Bed belong to the *Neospathognathodus celloni* Zone according to M. Kleffner (1990, personal commun.). A nearly identical conodont assemblage characterizes the overlying Wallington Limestone and, indeed, all of the overlying units assigned to the "Lower Clinton Group" ("Lower" Sodus, "Upper" Sodus, and Wolcott Formations). On the basis of this evidence, M. Kleffner (1990, personal commun.) is of the opinion that the entire interval above the base of the Seneca Park Bed is conformable and of Llandoveryan C-4 to C-5 age. Furthermore, he postulates a major unconformity within the Brewer Dock Member. However, there is seemingly no physical evidence for a major break below the Seneca Park Bed. Furthermore, the *Eocoelia* brachiopod zonation proposed by Zeigler (1966) suggests that these strata range from C-2 to C-4 age. An important ostracode zonal boundary occurs above the "Lower" Sodus Shale, whereas the Neagha–Brewer Dock–Wallington–"Lower" Sodus interval apparently belongs to the *Zygobolba excavata* Zone, a rather thin interval in the classic Pennsylvania succession (Ulrich and Bassler, 1923). This evidence argues against a major unconformity within the Brewer Dock Member. It is suggested herein that an unconformity may exist below the Reynales Limestone, and that the conodonts from the lower part of the Brewer Dock Member are reworked from the underlying Neagha Shale.



Figure 11. Reynales Limestone at Rochester, Monroe County, New York. A, Typical outcrop of Maplewood Shale (M) and lower beds of Reynales Limestone; thin limestone ledges comprise Brewer Dock Member (BD); Seneca Park Bed (S) (hematite) forms bed of creek above falls; ledges of Wallington Member (W) protrude from upper bank; Brewer Dock Member is about 1 m thick; Densmore Creek, Rochester, Monroe County, New York. B, Underside of calcisiltite bed beneath Seneca Park hematite bed, Brewer Dock Member, with ball-and-pillow deformation; note hammer for scale. C, Seneca Park hematite bed displaying small-scale tabular cross-stratification of hematitic skeletal grainstone; lens cap for scale. D, Photomicrograph (x15) of Seneca Park Bed showing hematite-impregnated and -coated skeletal (black) grains, including bryozoan (lower left) and crinoid columnar (top center) surrounded by sparry calcite cement; Genesee Gorge, Rochester, New York. E, F, Drill core sections (x0.8) showing upper Brewer Dock interval at Rochester, New York. E, Note lower beds rich in the brachiopod *Hyattidina* (h) overlain by laminated calcisiltite and base of hematitic Seneca Park Bed (split between lower and upper sections of core). F, Seneca Park Bed hematite with fossil fragments is capped by thin laminated calcisiltite. Core property of Hailey and Aldrich Corporation, Rochester, New York.

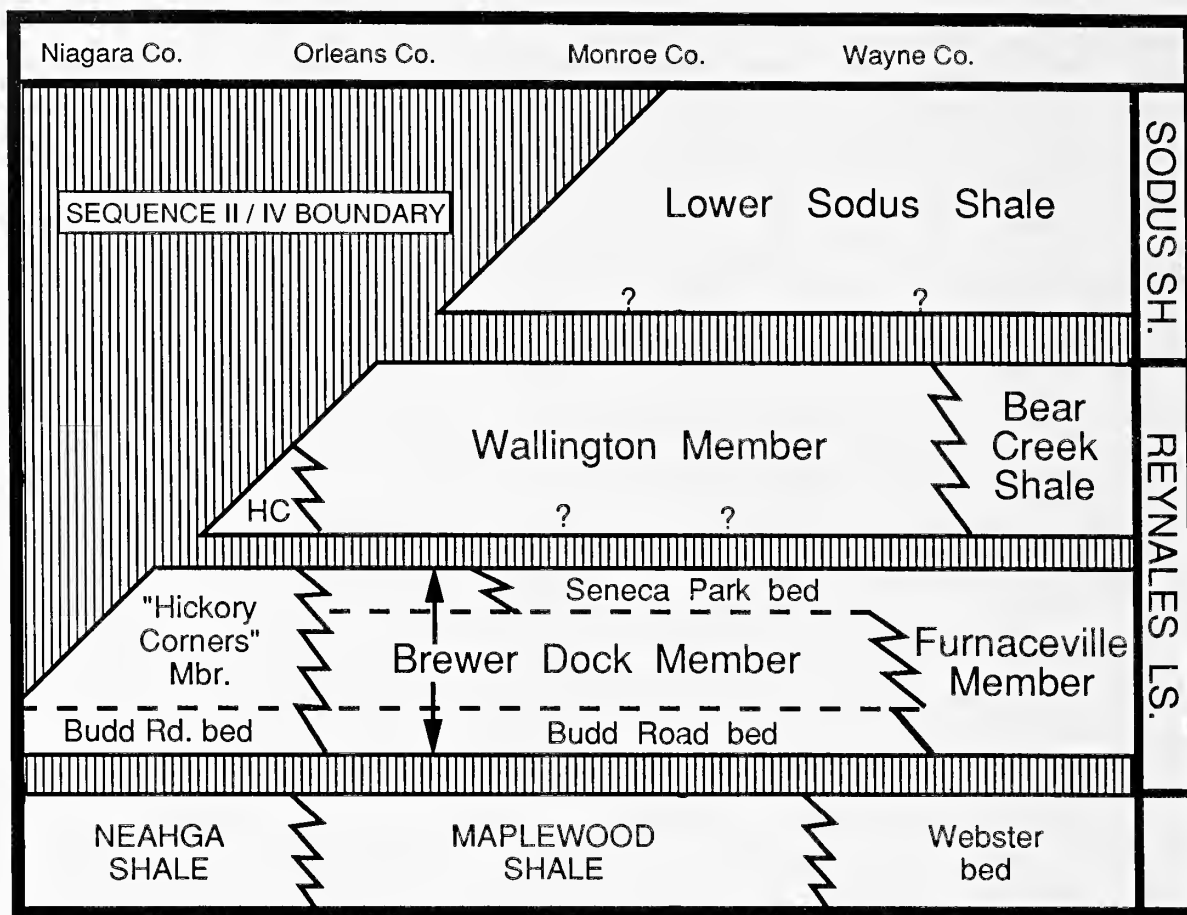


Figure 12. Summary chart of chronostratigraphic relationships of Reynales Limestone beds and members in western New York State.

Seneca Park Bed.—A 20 to 40 cm-thick bed at the top of the Brewer Dock Member has been assigned to the "Furnaceville Hematite" or "Iron Ore" (see Gillette, 1947; and Figures 11E, F, and 12). This hematitic limestone consists of a fossil-rich ore in which fragments of bryozoans, crinoids, and ostracodes, as well as intraclasts, have been replaced by hematite (Figure 11E, F). Restudy indicates that the so-called "Furnaceville Hematite" at Rochester is equivalent only to a part of the Furnaceville Member at the type section in Ontario, Wayne County, New York (LoDuca, 1988). In fact, the hematite at Rochester is equivalent only to the uppermost bed of the "true" Furnaceville Member which, in turn, is laterally equivalent to the entire Brewer Dock Member (see below). Hence this hematitic bed at Rochester is herein treated as a bed of the Brewer Dock Member, and termed the "Seneca Park Bed." It is not known how far this hematitic bed extends westward from the Rochester area. Drill cores from Albion, Orleans County, penetrate this interval and show no hint of a hematitic bed. However, a 20-30 cm-thick crinoidal grainstone bed appears at the appropriate position, about 1.0 m above the base of the Reynales Limestone. This crinoidal grainstone to nodular packstone band can be traced westward to the Niagara Gorge, where it lies immediately below the upper sequence boundary erosion surface (i.e., below the basal Second Creek Bed of the Williamson Shale). This unit always occurs approximately 0.5 to 1.0 m above the base of the Reynales Limestone, and forms a useful marker for the top of the Brewer Dock Member beyond the range of occurrence of the hematitic Seneca Park Bed in western New York (Figure 10). The

Seneca Park Bed and its lateral equivalent, therefore, are used herein to define the top of the Brewer Dock Member.

East of Rochester, the hematitic Seneca Park Bed is absent at Glen Edith on the east side of Irondequoit Bay. Detailed study in this region of the overlying Wallington Member indicates that the Wallington Member directly overlies the lower part of the Brewer Dock Member; the Seneca Park Bed is apparently absent because of non-deposition. Slightly farther east, in drill cores from Xerox Corporation property in Webster, New York, the entire Brewer Dock Member appears to be missing, and marker beds of the basal Wallington Member directly overlie the hematitic Webster Bed. At the Fruitland iron ore pit in Ontario Center, Wayne County, New York, the hematitic and phosphatic conglomerates of the Webster Bed are directly overlain by a 0.5 m-thick succession of hematitic limestone and shale that represents the type section of the Furnaceville Member. The upper portion of the type Furnaceville Member corresponds to the Seneca Park Bed of the Rochester Gorge. The thickness and internal stratigraphy of the Furnaceville Member closely match the Brewer Dock Member, and it is concluded that the two units are coeval. A very similar succession is seen eastward at Salmon Creek and in the Wallington and Wolcott drill cores (Gillette, 1947). In the Wolcott drill core, about a meter of hematitic limestone and interbedded shales occurs above the phosphatic Webster Bed (Figure 10). This interval appears to be a nearly complete, although thoroughly hematitized, version of the Brewer Dock Member.

Brewer Dock–Furnaceville Member correlation.—Detailed microstratigraphic analysis of the Brewer Dock and Furnaceville Members permits a virtual bed-for-bed correlation of six or seven units within this meter-thick interval (Figures 10, 12). These six or seven beds can be grouped into three very small-scale cycles, each of which has a basal, thin phosphatic calcarenite horizon that passes gradationally upward into greenish grey shales.

The first minor cycle of the Brewer Dock Member consists of the thin, phosphatic Budd Road Bed that ranges from about 2.0 to 5.0 cm thick. The Budd Road Bed is overlain by thin greenish-grey shale. This cycle is then overlain by a second phosphatic calcarenite horizon, again about 5.0 to 10.0 cm thick, which also passes upward into a greenish grey shale. This green clay shale ranges upward to 70 cm in thickness in one drill core from Monroe County. Elsewhere, it averages from about 20 to 30 cm in thickness. In turn, this shale is overlain by yet another phosphate granule-bearing horizon that passes upward into a brachiopod (*Hyattidina* and *Eocoelia*) pack- or grainstone (Figure 12). A distinctive 10 to 15 cm bed of calcisiltite (laminated pelletal grainstone) with prominent ball-and-pillow structures occurs above the *Hyattidina* bed in Monroe County localities (Figure 11B, E). This horizon forms a useful local marker, and it is present at Glen Edith where the overlying hematite is absent. The ball-and-pillow horizon is overlain by red, hematitic, bryozoan-rich grainstone of the Seneca Park Bed. A cap of silty calcareous green shale (a few cm thick) terminates this cycle (top of Figure 11F).

The three minor cycles of the Brewer Dock Member extend westward to the Niagara Gorge and can be used to differentiate the Brewer Dock Member from the overlying Wallington Member in the absence of the Seneca Park Bed. The lateral equivalent of the Seneca Park Bed, a crinoidal grain- or packstone, is also widely traceable and permits unambiguous recognition of the Brewer Dock–Wallington interval. Thus the so-called “Hickory Corners Member” of the Reynales Limestone (Kilgour, 1963) is simply an amalgam of the Brewer Dock Member and lower beds of the Wallington Member of the Reynales Limestone (Figures 10 and 13).

Each of the three small-scale cycles within the Brewer Dock Member can be viewed as a small-scale PAC or parasequence (see Goodwin and Anderson, 1985; Van Wagoner et al., 1988). These cycles were initiated abruptly by marine flooding that followed a relatively brief interval of sediment starvation recorded by phosphatic lags. Overlying brachiopod-rich pack- or grainstones then pass upward into greenish shales. The green shales appear to represent the shallowest water facies associated with each minor asymmetrical cycle. Presumably, these Maplewood-like shales, with a BA-2 biofacies (see below), represent minor progradational tongues of nearshore mud. The pack- and grainstones at the bases of the cycles contain a somewhat deeper water, BA-3 biofacies. Thus these small-scale cycles appear to be upward-shallowing. Taken collectively, however, the three minor cycles of the Brewer Dock Member seem to define an upward-deepening trend. In successive cycles, the greenish shales become less pronounced and the carbonates more prominent.

Wallington Member.—The Wallington Member, named for exposures on Salmon Creek at Wallington, Wayne County, New York (Hartnagel, 1907), consists of about 4.0 to 6.0 m of dolostone, commonly cherty brachiopod/crinoid pack- and grainstone, pelletal grainstone (calcisiltite), and greenish grey shale (see Paxson, 1985). The base of the Wallington Member of the Reynales Limestone is defined at the base of a phosphate granule-bearing thin grainstone bed that overlies the Seneca Park Bed. This basal marker bed appears in virtually all

sections of the Wallington Member.

The Wallington Member is similar to the Brewer Dock Member and may be subdivided into about six carbonate-to-shale cycles, or PACs, that fine upward; the Wallington Member, as a whole, appears to deepen upward. The base of each cycle can be recognized by a calcarenite bed, in many cases with pentamerid brachiopods (Figure 11A). Six pentamerid-rich grainstone beds recognized in the Genesee Gorge define the bases of minor (PAC-like) asymmetrical carbonate-to-shale cycles (Figure 10). These are positioned at the base (basal Wallington carbonate bed), approximately 1.4 m, 2.0 m, 2.8 m, 3.2 m, and 4.0 m above the base of the formation, respectively. Several of these tend to be cherty, at least at some locations. The most prominent pentamerid-bearing grainstone bed forms the base of the fifth cycle and occurs about 1 m below the contact with the overlying “Lower” Sodus Shale. This unit includes approximately 60 cm of pentamerid-rich crinoidal grainstone with internal, amalgamated, hummocky, normally graded beds with shell-rich calcarenites at the bases that grade upwards into thin calcisiltites. Overlying this bed is 45 cm of greenish grey shale that may represent a somewhat deeper-water environment, as opposed to the more typical greenish shales at the base of the formation. Overall, this cycle appears to represent a strong transgressive episode during deposition of the Reynales Limestone. The uppermost cycle of the Wallington Member at the Genesee Gorge consists of a 15–20 cm bed of dark-stained crinoidal–stromatoporoid–brachiopod-rich limestone. This cycle appears to thin eastward and merge into the 10–20 cm-thick “Sterling Station Hematite” (Gillette, 1947) that marks the top of the Reynales Limestone and the equivalent Bear Creek Shale in Wayne and Oswego Counties.

Westward from the Genesee Gorge area, outcrops of the Wallington Member are infrequent and poorly exposed, although *Pentamerus*-rich limestones are known from scattered, patchy outcrops in the bed of Salmon Creek between Brockport and Spencerport, New York, and drift boulders of *Pentamerus*-rich Reynales Limestone are common in the area around Clarendon. A drill core from the town of Albion shows 1.5–2.0 m of nearly homogeneous crinoidal grainstone. This unit is composed mainly of pentalobate crinoid columnals, although brachiopods, particularly *Hyattidina*, are abundant throughout this portion of the section. This grainstone is the lateral equivalent of the lower greenish shale and carbonate bands found in the basal meter of the Wallington Member at Rochester, and it persists westward at least to Lockport, where about 120 cm of grainstone is present. At Lockport and Middleport, crinoidal pack- and grainstone is the predominant lithology. Neither the Brewer Dock nor the Wallington Member of the Reynales Limestone have previously been recognized in this area, and the term “Hickory Corners Member” has been used to refer to the entire Reynales Limestone in Niagara County.

The Wallington Member maintains a relatively uniform internal stratigraphy east of Rochester (see Figures 10, 12). The shale intervals that form the upper parts of the six minor cycles of the Wallington Member become increasingly pronounced and thicker in the vicinity of the type section of the Wallington Member on Salmon Creek (east) in central Wayne County. The second chert-rich pentamerid-bearing band, about 120–150 cm above the base of the unit, becomes increasingly rich with these brachiopods eastward to the type section. East of the type area, this interval loses the pentamarids but remains cherty at least to the area of Wolcott. The upper two pentamerid beds of the Rochester Gorge, which are the most condensed crinoidal grainstones, also persist for the longest distance to the east.

Bear Creek Shale.—The greenish grey shales of the Wallington Member at Bear Creek in eastern Wayne County have thickened so

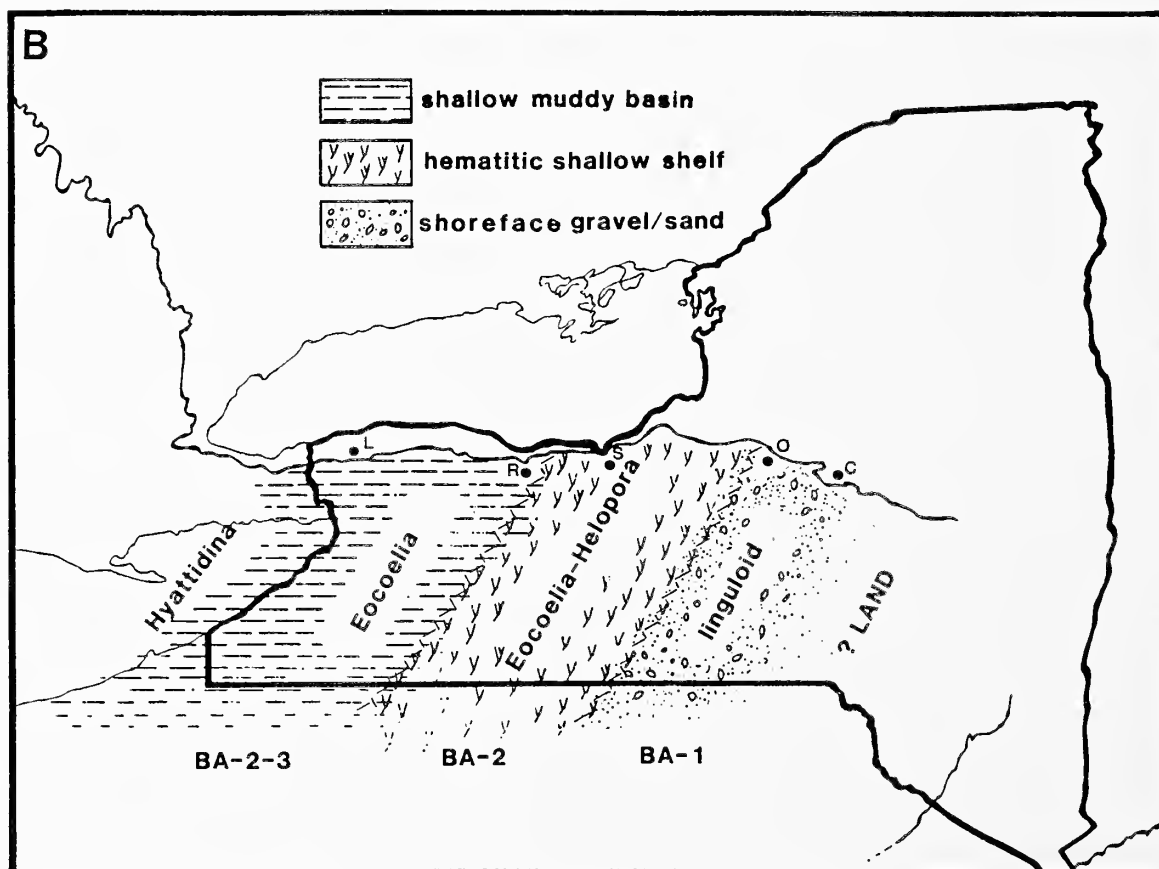
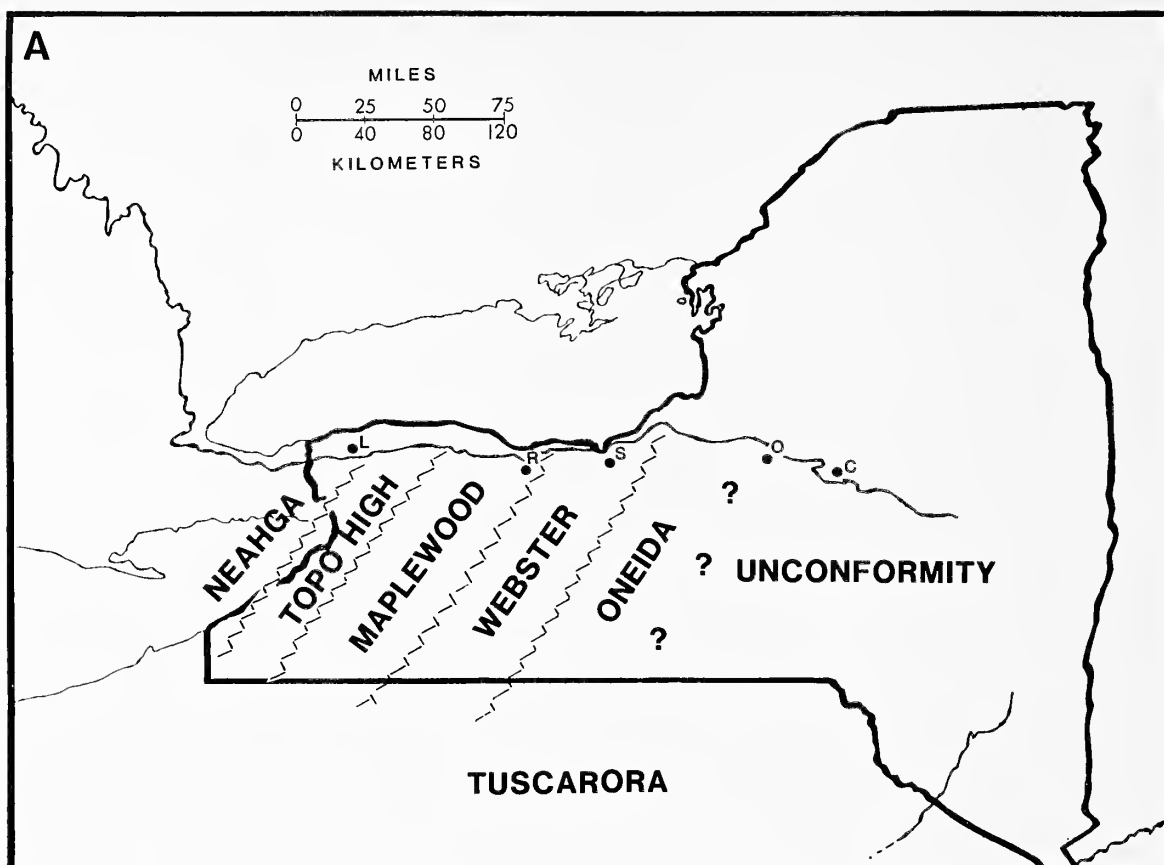


Figure 13. Litho- and biofacies maps of the Neahga-Maplewood interval. A, Lithofacies map of Neahga-Maplewood interval; note northeast-southwest strike of facies belts and minor high area separating Neahga and Maplewood facies; wavy lines represent approximate lateral boundaries. B, Paleogeographic map showing distribution of biofacies; benthic assemblages (BA) and names of prominent fossils are indicated.

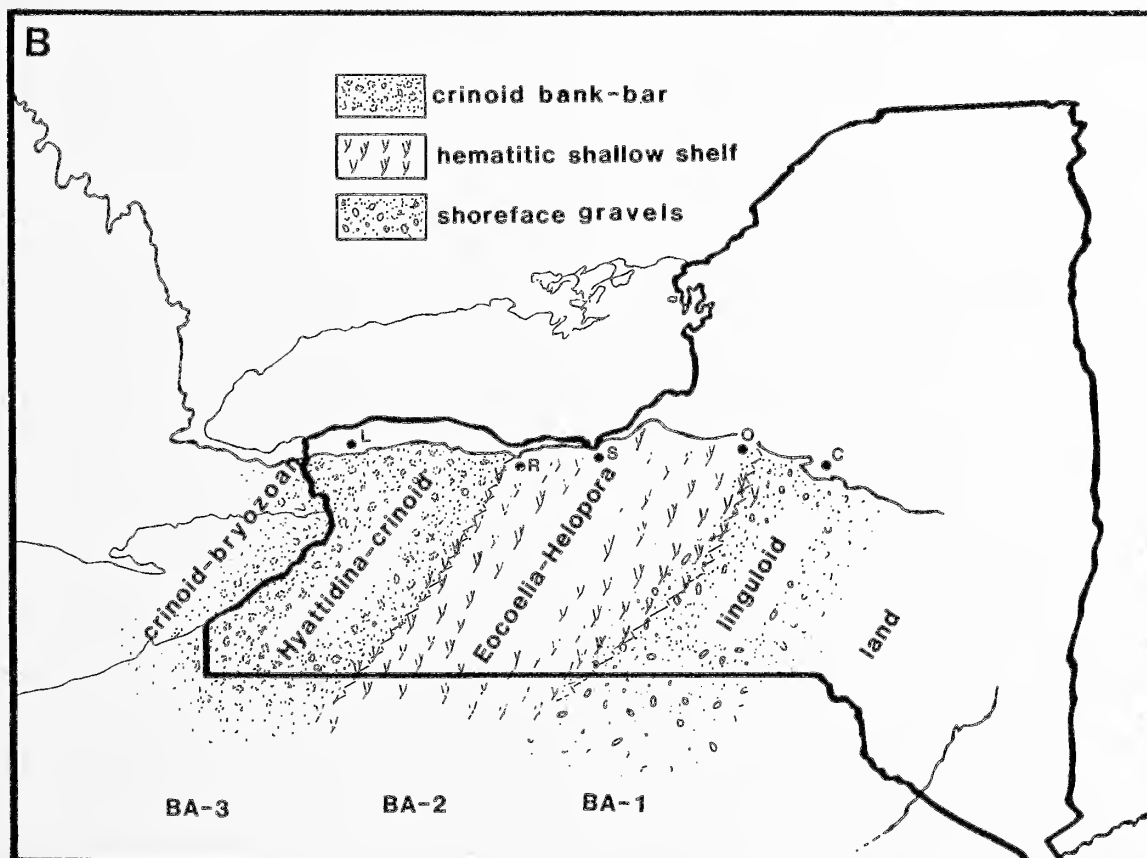
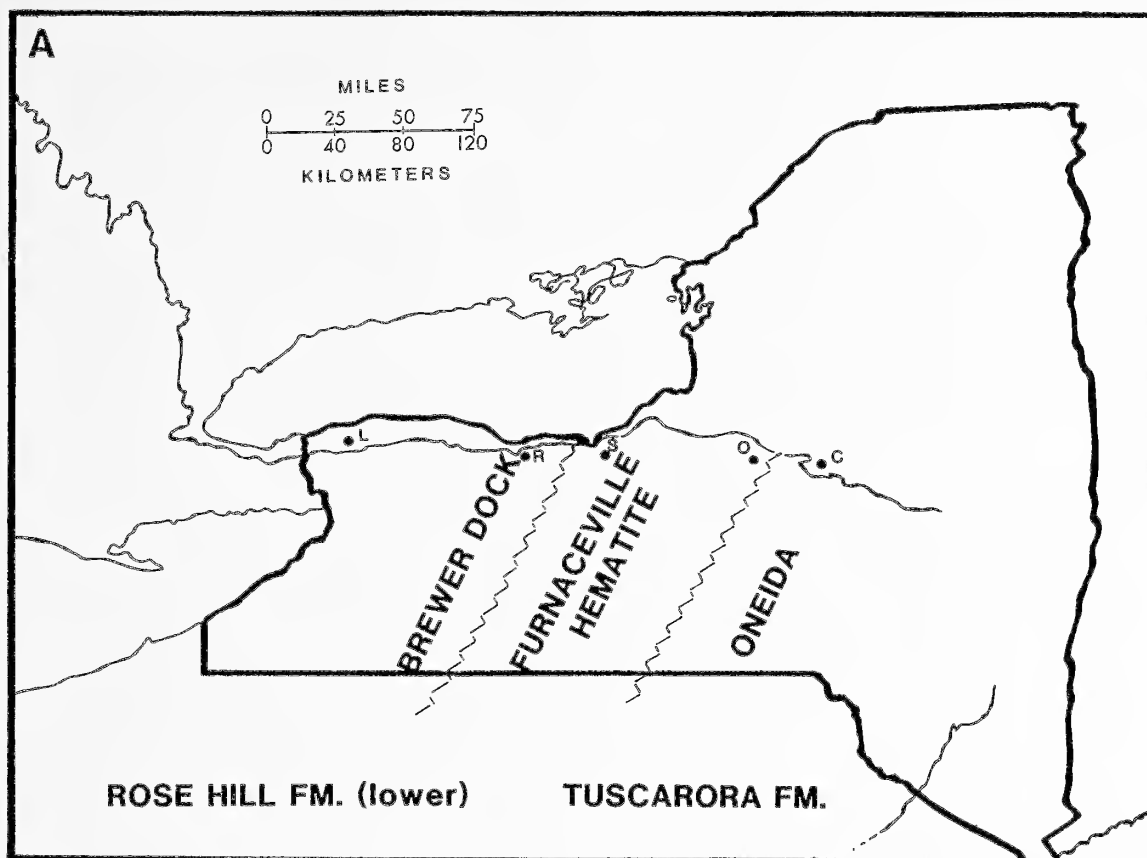


Figure 14. Litho- and biofacies maps of the Reynales Limestone and equivalents. A, Lithofacies map for lower part of the Reynales Limestone (Brewer Dock-Furnaceville) interval. Local names of lithostratigraphic units are indicated. B, Paleogeographic map showing inferred distribution of biofacies; benthic assemblages (BA) and prominent fossils are indicated.

much that the unit has become more than half shale. This interval was designated the "Bear Creek Shale" by Chadwick (1918). At the type locality, the Bear Creek consists almost entirely of shales with very thin, argillaceous, pyritic limestones. These have an *Eocoelia hemispherica*-dominated fauna.

Lithofacies, biofacies, and lateral changes within the lower part of the Clinton Group of western New York

Only three units in the "Lower Clinton Group" can be traced from west-central New York to the Niagara region. However, these permit some assessment of lateral facies changes (see Figures 12-14).

The first of these is the Maplewood-Neahga Shale interval. At its easternmost margin, the interval appears to merge into the basal bed of the Oneida Conglomerate and is represented by a thin, pale greenish grey sandstone and quartz pebble conglomerate, typically less than 30 cm thick, that sharply overlies sandstones attributed herein to the Kodak Sandstone of the Medina Group (Figure 13). The unit contains some trace fossils, including *Skolithos*-like burrows and body fossils of linguloid brachiopods and scattered ostracodes, among them *Zygobolba*. This interval is traceable from Oneida County near Lakeport at Oneida Lake westward approximately to central Oswego County, where it thins slightly and contains abundant multigenerational phosphatic clasts. In this area and to the west, the interval is referred to as the "Webster Bed." The eastern Oneida Conglomerate represents a relatively sediment-starved, nearshore gravel. Tabular cross-bedding suggests current deposition. The sandy layers perhaps represent slightly lower energy environments between gravel bars. These areas were inhabited by linguloid brachiopods and other burrowing organisms.

The hematitic and phosphatic conglomerate of the Webster Bed is probably equivalent to much or all of the Maplewood Shale (Figure 13A). Quartz pebbles and granules occur commonly within the Webster Bed at least as far west as central Wayne County. Fossils are rare within the conglomerate but include phosphatized gastropods, linguloid and *Eocoelia* brachiopods, and the bryozoans *Phaenopora* and *Helopora*. In contrast to the Oneida Conglomerate, which represents a very nearshore fossil assemblage (benthic assemblage 1; BA-1), the Webster Bed shows elements of an *Eocoelia* or BA-2 biofacies (Figure 13B).

The hematitic and phosphatic conglomerate facies of the Webster Bed seem to represent an extremely condensed, shallow-shelf deposit. During deposition of this facies, relict sediments probably covered a broad tract of shelf that extended at least 50 km perpendicular to the facies strike. Phosphatic coatings and mineralized steinkerns in the upper few centimeters of reworked sediment developed, in part, after cannibalization of the underlying sands of the Medina Group. This gravel and the equivalent lower part of the Oneida Conglomerate represent transgressive lag deposits that were associated with a major relative sea-level rise (basal sequence II) that followed a major sea-level fall, during which quartz pebbles and sand were transported toward the basin center.

In northeastern Monroe County along a line that trends approximately N45°E, the thin phosphatic conglomerate of the Webster Bed is abruptly transitional to the main mass of Maplewood Shale (Figure 13A). Within less than 10 km, the shale expands from a thin parting to over 7.0 m. A thin phosphatic pebble bed (Densmore Creek Bed) still occurs at the base of the Maplewood Shale, and extends westward to form the base of the correlative Neahga Shale. The phosphatic bed con-

tains rare brachiopods, including *Hyattidina*, in the Rochester area. Westward, near Lockport, *Hyattidina* becomes very abundant and, near St. Catharine's, Ontario, the basal bed expands to a 30 cm-thick crinoidal sandy carbonate with some *Hyattidina*, as well as bryozoans and a more diverse brachiopod assemblage typical of the overlying Reynales Limestone. The *Hyattidina* biofacies is believed to be an inner shoal BA-2 to BA-3 fossil assemblage, whereas the more diverse, bryozoan-rich sandy limestone at the westernmost exposures of the Neahga interval near St. Catharine's appears to represent a BA-3 shoal-type environment very similar to that of the overlying Reynales Limestone.

The main mass of the Maplewood and Neahga Shales is more or less undifferentiated green and dark grey clay shale. Near the eastern limit of the outcrop belt, the shale contains a few thin siltstone bands, but these rarely exceed a centimeter in thickness. Thin stringers of phosphatic granules observed at widely scattered levels in Rochester and Glen Edith suggest occasional storm transport of phosphatic material from nearby shoals to the northeast. The lack of any internal cyclicity within the Maplewood and Neahga Shales suggests that the shales represent a relatively brief interval of time. Thus while multigenerational phosphatic conglomerates and coarse pebble gravels were deposited in a sediment-starved shelf area to the northeast, the Maplewood and Neahga muds were rapidly deposited in low-energy traps associated with minor subsiding depocenters to the west. The high clay content of both shales is somewhat enigmatic and suggests a relative paucity of sand-sized material available for deposition. Complete crinoids and possible soft-bodied organisms on certain bedding-planes suggest rapid sedimentation of mud layers within the Maplewood Shale; this evidence of episodically high rates of accumulation is not otherwise apparent from examination of the unit. Dark grey to greenish coloration indicates deposition of the muds under reducing conditions or high accumulation rates, and the absence of coarser storm layers suggests low-energy environments within the Neahga and Maplewood basins. Yet the uniform occurrence of diverse sporomorphs suggests a proximal position, as does the presence of rare eurypterid cuticle within the Maplewood Shale.

The Maplewood Shale uniformly has a very sparse *Eocoelia* to *Lingula*-bearing (BA-2) assemblage. The Neahga Shale, or western facies of the Maplewood, contains a slightly greater diversity of associated brachiopods, although *Eocoelia* still dominates. The occurrence of rare *Eoplectodonta*, *Dalejina*, and other brachiopods at the Niagara Gorge indicates a more distal BA-2 to marginal BA-3 position. The basal sandy limestone bed at the westernmost outcrop of the Neahga Shale suggests that the unit might undergo a lateral facies change from green shale to carbonates. If so, it appears that the lower portions of the Neahga and Maplewood Shales probably represent the deepest water conditions (BA-3), and that these units as a whole display a shallowing-upward trend typical of PAC cycles (Goodwin and Anderson, 1985). The Neahga and Maplewood Shales are abruptly overlain by the thin phosphatic limestone of the Budd Road Bed, which carries an *Eocoelia*-dominated (BA-2) fossil assemblage in the east. In Monroe County, it represents a typical "pearly bed," or dense *Eocoelia* packstone, with mixed *Helopora* bryozoans. Westward in Niagara County, this basal bed has a *Hyattidina* fauna associated with very abundant phosphatic pebbles and granules. Hence the bed comes to resemble closely the Densmore Creek Bed that forms the base of the Maplewood and Neahga Shales. This bed represents an interval of relative sediment starvation, during which authigenic phosphate formed either within fossils or as small nodules in the upper few centimeters of sediment. A micro-oxidizing zone immediately above the reducing greenish grey muds

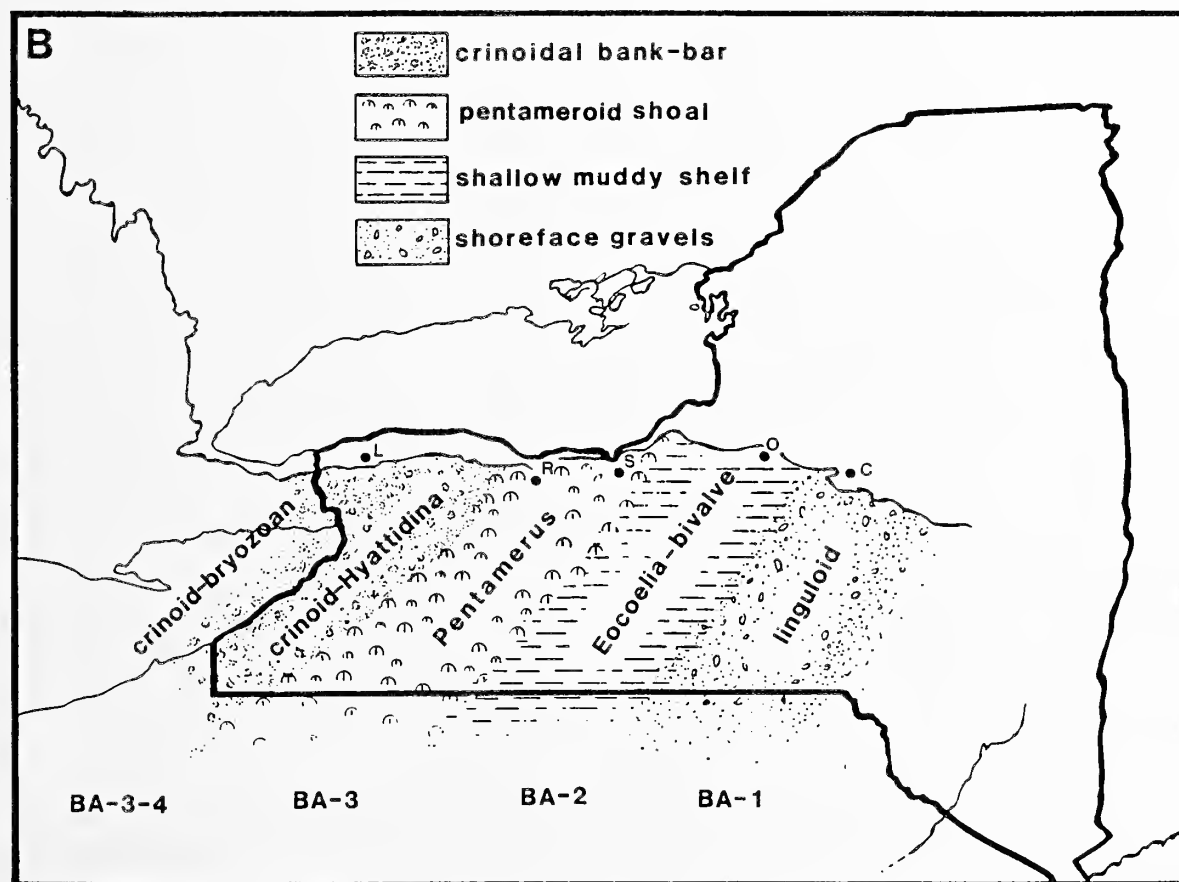
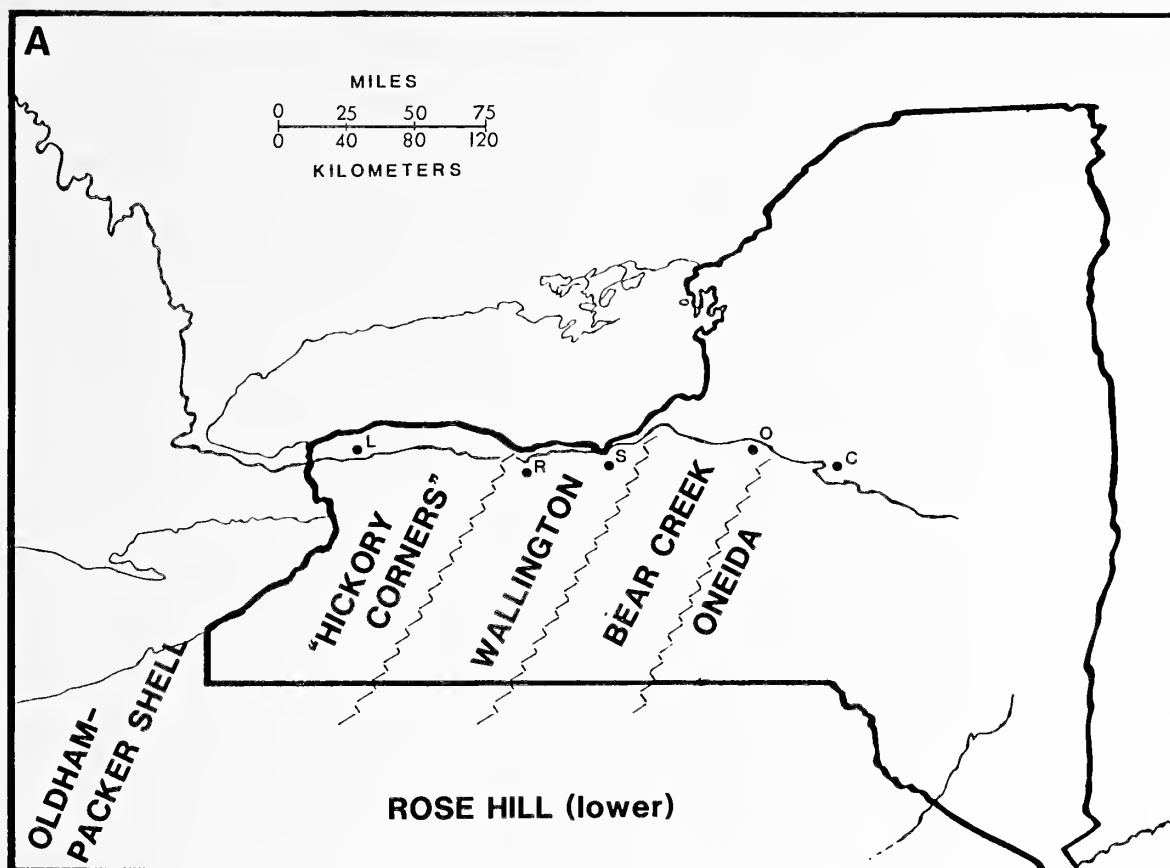


Figure 15. Litho- and biofacies maps for the upper part of the Reynales Limestone and equivalents. A, Lithofacies map for the upper part of the Reynales Limestone interval (Wallington-Bear Creek). Local names of lithostratigraphic units are indicated. B, Paleogeographic map showing inferred distribution of biofacies; benthic assemblages (BA) and names of prominent fossils are indicated.

probably provided a site for nucleation of phosphate nodules. These were reworked on the sea bottom during a period of non-sedimentation and minor erosion.

The Brewer Dock Member provides another facies transect from central to western New York. As the Maplewood-Neahga Shale transects, it suggests a westward change from BA-1 shoreline facies at about Oneida County into BA-3 or even BA-4 offshore deeper-water assemblages westward in Niagara County (Figure 14A, B).

In its eastern outcrop belt, the Brewer Dock Member is equivalent to the Furnaceville Member. The lowest beds of the latter are oolitic, phosphatic hematite beds that directly overlie the somewhat hematitic, phosphatic conglomerate of the Webster Bed. The fauna, where present within these beds, is extremely sparse, but may include the brachiopods *Eocoelia* and *Coolinia*. The upper beds of the Furnaceville Member (equivalent to the third cycle of the Brewer Dock), which typically represent the most hematitic portion of the unit, grade westward into the 20-30 cm-thick thoroughly hematized coquinoid limestone of the Seneca Park Bed. The Seneca Park Bed is composed almost entirely of the brachiopod *Eocoelia*. This coquinoid ledge may give way eastward to a basal shale tongue of the Bear Creek Shale in Oswego County.

Westward in Monroe County, the Furnaceville Member divides into a number of cyclic packages within the Brewer Dock. Only the uppermost cyclic unit remains hematitic as far west as Rochester, where it is referred to as the Seneca Park Bed. The lower portion of the Brewer Dock is approximately 40 to 50 cm thick, and contains two sharp-based phosphatic grainstone beds overlain by green Maplewood-like shale with a sparse *Eocoelia* (BA-2) fossil assemblage. The upper cycle of the Brewer Dock Member has diverse bryozoan- and *Hyattidina*-bearing limestone at its base, and a hematitic grainstone unit (Seneca Park Bed) packed with fragmented *Eocoelia* shells, crinoids, and bryozoans at its top.

The Brewer Dock Member still can be subdivided into its three component cycles in western sections, and the lower half is still the most shaly. In the drill core from the Albion landfill site, *Hyattidina* brachiopods appear with *Eocoelia* in the thin phosphatic limestones and shales of the lower part of the Brewer Dock Member. The upper, more compact limestone loses all traces of hematite and has a crinoidal pack- or grainstone lithology with abundant *Hyattidina* shells scattered throughout. Portions of the Brewer Dock Member that bear *Hyattidina* shells at Rochester rapidly change into crinoid grainstone facies to the west in Orleans County.

Still farther west in the Niagara County region at the type section of the Hickory Corners Member, the lower argillaceous portion of the Brewer Dock Member is dominated by *Hyattidina* with scattered *Eocoelia* (BA-2 to BA-3 boundary fauna), and begins to display a diversity of other brachiopods and some thin ramose bryozoans (Figure 14B). Some of the limestone layers become crinoidal pack- and grainstone. In this area the uppermost cycle has changed into a somewhat nodular crinoidal grain- and packstone with rugose corals; scattered *Hyattidina* and a diversity of other brachiopods, such as *Platystrophia* and *Dalejina*; fenestrate bryozoans; nautiloids; and crinoids of various types (Eckert, 1989). The upper portion of this ledge may be capped by a 5-10 cm crinoidal grainstone that corresponds to the hematite of the Seneca Park Bed. At the westernmost localities at Niagara Gorge, the lower portions of the Brewer Dock Member become *Hyattidina*-rich, crinoidal pack- and grainstones, whereas the upper portions become argillaceous and nodular pack- and wackestones that probably represent relatively offshore (BA-3) conditions. Hence, in the Brewer Dock Member, there is a westward shift from BA-2 or even BA-1 assem-

blages at Oneida County into BA-3 grainstones with dominant *Hyattidina*, and finally into more diverse, offshore, nodular wacke- and packstones with relatively diverse coral, bryozoan, crinoid, and brachiopod assemblages.

The only other "Lower Clinton Group" unit that can be traced over an extensive distance is the lower part of the Wallington Member (Figure 15A). Its lateral correlative can be traced approximately from Lakeport on Oneida Lake, where the entire Wallington equivalent is represented by about 50 cm of very hematitic, *Eocoelia*-bearing limestones and shales assigned to the Bear Creek Shale. In eastern Wayne and Oswego Counties, outcrops of the Bear Creek Shale average about 3 to 4 m in thickness and consist of dark grey to greenish grey, slightly silty shale with a few thin limestone beds notably at the base, near the middle, and near the top of the unit. The dominant fauna consists of *Eocoelia intermedia* and a variety of small bivalves such as *Ctenodonta*, *Pyrenomoeous*, and *Modiolopsis*. The limestones contain extremely rare pentamerids, as well as *Dalejina*, *Coolinia*, and various bryozoans and crinoids. Complete articulated specimens of crinoids belonging to three new camerate species and *Dendrocrinus* were obtained at Bear Creek from the upper half-meter of shale (see Eckert, 1989).

The percentage of shale partings within the Wallington Member decreases westward. At the type section on Salmon Creek, the unit consists of a thin green shale overlain by about 30 cm of *Eocoelia*- and pentamerid-bearing hematitic limestone. This is followed by a highly shaly section with thin nodular calcisiltite beds that are overlain by the main pentamerid-bearing beds of cherty, blocky limestones. The uppermost beds again are shaly, except for the top hematitic limestone. The *Pentamerus*-bearing beds at Rochester appear to correlate with shaly portions of the Wallington Member farther east, and this indicates a general progression from *Eocoelia*-rich shales and mudstones of Oneida and eastern Wayne Counties to pentamerid-rich limestones of western Wayne and Monroe Counties. These lateral biofacies trends appear to corroborate the typical BA-2 to BA-3 onshore-offshore gradation observed in many Silurian successions (Figure 15B).

The westernmost exposures of the Wallington Member are equivalent to the upper units of the Hickory Corners Member. These are mostly compact crinoidal pack- and grainstones with some cross-bedding. Minor chert nodules appear near the middle parts of the section and probably correspond to the cherty layers seen at Wallington and Rochester. Pentamerids are notably rare or absent west of Monroe County, where the main mass of the Wallington Member is strictly crinoidal grainstones with relatively abundant *Hyattidina* brachiopods. This phenomenon suggests that pentamerids may be associated with the inner shoal margins adjacent to BA-2, *Eocoelia*-bearing mudstones. These, then, grade offshore into crinoidal facies containing the *Hyattidina* fauna. Observation of further westward facies progression within the Wallington Member is impossible because of regional beveling of the unit by the overlying unconformity that forms the base of the "Upper Clinton Group."

Conclusions

Detailed regional study of the "Lower Clinton Group" in western New York and Ontario supports the following conclusions:

1. The "Lower Clinton Group" is an unconformity-bounded sequence with a basal, regionally beveled surface and a major overlying

angular unconformity that forms the base of the Llandoveryan (C-6) Williamson Shale of the "Upper Clinton Group."

2. The Thorold Sandstone should not be included as the basal unit of the Clinton Group. The Thorold Sandstone *sensu stricto* is found beneath the basal Clinton unconformity westward from Niagara County, New York, to St. Catharine's, Ontario. Eastward from Niagara County, the units that overlie the Thorold Sandstone include the 2.0 to 3.0 m, reddish, ostracode-bearing Cambria Shale and the 2.0 to 5.0 m of greenish to slightly reddish grey Kodak Sandstone. These units intervene between the Thorold Sandstone and the basal part of the Clinton Group. The Thorold Sandstone, overlying Cambria Shale, and Kodak Sandstone all appear to be relatively conformable with one another, and therefore are herein included in the uppermost Medina Group and removed from the Clinton Group. These sandstones and shales below the Clinton Group are everywhere white to pale greenish as a result of post-depositional leaching apparently associated with the overlying basal unconformity of the Clinton Group.
3. The Clinton Group is bounded at its base by a phosphatic or quartzose conglomeratic layer. In the east, this constitutes a phosphate-bearing quartz pebble bed of the Oneida Conglomerate; in Wayne County, it consists of a slightly hematitic, phosphatic conglomerate termed the "Webster Bed." In Monroe to Niagara County, it is a thin (10-20 cm-thick) phosphatic unit (Densmore Creek Bed). From Lockport in Niagara County westward to its erosional truncation near St. Catharine's, Ontario, the base of the Clinton Group is a thin (5-30 cm), sandy, dark-stained calcareous sandstone with abundant *Hyattidina* and other fossils, and is considered to be a local facies of the Densmore Creek Bed.
4. The Maplewood and Neahga Shales are laterally coextensive and do not appear to be differentiable at any location. They were, however, deposited in different minor troughs that trended approximately northeast to southwest, and were separated by a central high that extended approximately southwest from the area of Lockport, New York, to Grand Island, New York. These trends are also subparallel to the eastward feather-edge of the Maplewood Shale that strikes southwest through western Monroe to Allegany County.
5. The Maplewood Shale pinches out abruptly along the aforementioned line and passes laterally into the slightly hematitic, phosphatic, multigenerational Webster Bed. This transition appears to represent a change from a very shallow, sediment-starved shelf to nearshore gravel. The Maplewood and Neahga Shales were deposited in relatively shallow, although poorly oxygenated, basins as inner-shelf muds. These units and their lateral equivalents range from BA-1 (linguloid-trace fossil) to outer BA-2 *Eocoelia* community biofacies.
6. The Maplewood-Neahga Shales are everywhere separated from the overlying Reynales Limestone by a thin phosphatic horizon, herein designated the "Budd Road Bed". This unit forms the base of the Reynales Limestone, and therefore constitutes the basal unit of the Hickory Corners Member, as previously designated by Kilgour (1963) in Niagara County, and the base of the Brewer Dock Member in Monroe County. East of Monroe County, the phosphatic Budd Road Bed appears to merge with the underlying phosphatic conglomerate of the Webster Bed, becomes hematitic, and forms the base of the Furnaceville Member. The lower part of the Brewer Dock Member contains three minor (20-100 cm) shallowing-

upward cycles that typically have phosphatic, fossiliferous, and locally hematitic limestones at their base and grade upward to green shale. The three cycles can be traced regionally, and each shows an internal westward progression from a shallow-water, nearshore biofacies and lithofacies in Oneida to Wayne Counties to a more offshore biofacies (BA-3 to BA-4) with diverse brachiopod, bryozoan, and coral assemblages in western Niagara County.

7. Although the details are not as firmly established for the overlying Wallington Member of the Reynales Limestone, it too can be traced west from nearshore hematitic sandy limestone beds through slightly offshore greenish grey shales into shell-rich carbonates. In general, both the Brewer Dock and Wallington Members show a biofacies progression from BA-2 (*Eocoelia*-bearing shales and sandy limestones) through BA-3 (pentamerid or *Hyattidina*-bearing crinoidal pack- and wackestone beds); and finally, in the case of the Brewer Dock Member, into nodular argillaceous limestone with a diverse marginal BA-4 bryozoan-dominated, brachiopod-coral assemblage. These lateral facies shifts appear to corroborate the models of earlier workers such as Ziegler et al. (1968).
8. Finally, the "Lower Clinton Group" appears to display a general upward-deepening trend. In terms of sequence stratigraphy, the basal part of the Maplewood and Neahga Shale appears to represent a relatively shallow-water interval during the initial transgression. Overlying phosphatic limestones of the Hickory Corners or the Brewer Dock Members appear to represent sediment-starved conditions associated with the increased rate of sea-level rise. Overlying limestone and shales may represent relative highstand conditions.

The Maplewood-Neahga Shale through Reynales Limestone succession represents one fourth-order subsequence within the "Lower Clinton Group" (sequence II). This subsequence is capped by a thin oolitic hematite, the Sterling Station Bed. A second subsequence, composed of the "Lower" and "Upper" Sodus Shales and overlying Wolcott Limestone, was removed by late Llandoveryan erosion in western New York. It is not considered in detail in this report. This subsequence in many ways resembles the lower one, as it is a shale-dominated cycle that passes upward into fossil-rich carbonates. Superimposed on these two subsequences are minor shallowing-upward cycles that consist of basal carbonates that pass upward into greenish grey shales. In western New York, nodular, shaly limestone passes upward into grainstones. These thin (< 1.0 m) parasequences fundamentally appear to be upward-shallowing cycles, and are widely correlative. These minor cycles resemble the PACs of Goodwin and Anderson (1985) and form groupings that seem to constitute fifth-order cycles, such as those represented by the Brewer Dock and Wallington Members.

Acknowledgments

We thank W. Goodman, B. LoDuca, J. Eckert, and B. Lin (Eckert) for field assistance and valuable discussion of ideas. Research was funded by grants from the donors to the Petroleum Research Fund of the American Chemical Society and the Audubon Society, and an honorarium from the New York State Geological Survey. We also thank R. Libbe, M. Johnson, A. Boucot, and C. Teichert for critical reviews, H. Jacob and L. Stockmaster for manuscript preparation, and W. Taylor for photographic assistance. The Petroleum Research Fund supplied \$1,500 toward publication of this report.

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The last olenacean trilobite: *Triarthrus* in the Whitby Formation (Upper Ordovician) of southern Ontario

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Abstract

The Whitby Formation is a 25-90 m sequence of Upper Ordovician (Maysvillian) recessive shales underlain by the Cobourg Formation (Edenian) and overlain by the Georgian Bay Formation (Richmondian) in southern Ontario. The lower member consists of 5-20 m of dark grey bituminous shale, and the upper member includes 20-80 m of light and medium grey shale. The Whitby Formation was deposited under the influence of storm activity in moderately shallow water within a short-lived foreland basin, the Utica Basin (new name), that was formed by lithospheric downwarp in response to loading by Taconian overthrusts. A detailed biostratigraphy of these shales has been difficult because outcrops are poor. Nineteen continuous drill cores now provide data on the distribution of five species of the olenid trilobite *Triarthrus* and of graptolites.

The distribution, diversification, and extinction of *Triarthrus* were strongly influenced by phases of the Taconian Orogeny. A *Triarthrus* Biofacies shifted from Franklinian and Edenian slope settings in the Taconic Trough of central New York to Maysvillian epicratonic settings in the Utica Basin of Ontario and Quebec when fine-grained sediment from the emergent Taconic Arc was swept across the craton. Specimen abundance of each species of *Triarthrus* in the Whitby Formation closely follows shale colors which, in turn, most likely indicate different oxygen levels of the sediment. The *Triarthrus* Biofacies comprises a *T. eatoni* Sub-biofacies in dark grey shales, a *T. canadensis* Sub-biofacies in medium grey shales, and a *T. rougensis* Sub-biofacies in light grey shale. *Triarthrus* became extinct in North America as prograding coarse clastics of the Queenston Delta terminated the *T. rougensis* Sub-biofacies, the last remnant of the *Triarthrus* Biofacies.

Triarthrus comprises two subgenera: *T. (Triarthrus)* Green (type species, *T. beekii* Green, 1832) with six species, and *T. (Danarcus)* n. subgen. (type species, *T. glaber* Billings, 1859) with two species. The *Balnibarbiinae* Fortey, 1974, is considered a junior synonym of the *Triarthrinae* Ulrich, 1930.

Introduction

The extinction of the trilobite *Triarthrus* in the Late Ordovician spelled the demise of the Family Olenidae and the Superfamily Olenacea, and marked the end of oleniid dominance of slope and outer platform shale biofacies. This hegemony had lasted since the Late

Cambrian (Cisne, 1973; Fortey, 1975; Taylor, 1977; Ludvigsen and Westrop, 1983a).

Trilobites of the Superfamily Olenacea were abundant, widely distributed, and quite diverse in the Late Cambrian. A variety of families are known from Steptoean and Sunwaptan strata of North America (Ludvigsen and Westrop, 1983b), but few of these families survived the Cambrian. By the end of the Middle Ordovician, only a single subfamily, represented by a single genus, remained. *Triarthrus*, the last olenacean trilobite (Ludvigsen and Tuffnell, 1983), first appeared in the Franklinian Stage of eastern North America (upper Mohawkian Series of Sweet, 1988), and it became extinct some twelve to fifteen million years later in the latest Maysvillian or the early Richmondian.

A few species of *Triarthrus* are found in Ashgillian strata of northern Europe and in China. However, a species-based biostratigraphy is possible only in southern Ontario, where the genus is represented by a variety of species with known vertical ranges at many localities.

The taxonomy of all species of *Triarthrus* from eastern North America is revised in this paper. In addition, the reasons for the decline and demise of *Triarthrus* are clarified through biostratigraphic analysis of the Whitby Formation and correlative shale units in Ontario, Quebec, and New York State.

Sources of data

Exposures of the recessive Whitby Formation are mediocre—a fact that has frustrated detailed stratigraphic and paleontologic investigations of this shale unit. Short natural exposures are restricted to lakeshores and to a few creek beds. Artificial exposures in roadcuts, quarries, and building excavations are somewhat better, but no more than a few meters of strata are exposed in any one area.

In the early 1980s, the Ontario Geological Survey (OGS) began an investigation of the petroleum potential of various bituminous shale units in Ontario; one of these was the lower Whitby Formation. During commercial operations in the last century, oil shales now assigned to the lower Whitby Formation were reported to have produced an astonishing seven gallons of petroleum per ton of shale, according to Logan (1863). The OGS drilled nineteen continuously cored holes through all or most of the Whitby in four areas of southern Ontario: the Ottawa, Toronto, Collingwood, and Manitoulin areas. In addition, single holes were drilled in the Bolton and Corbetton areas (Figure 1). In all, some 1000 m of 4.5-cm-diameter core were sampled for megafossils. More than

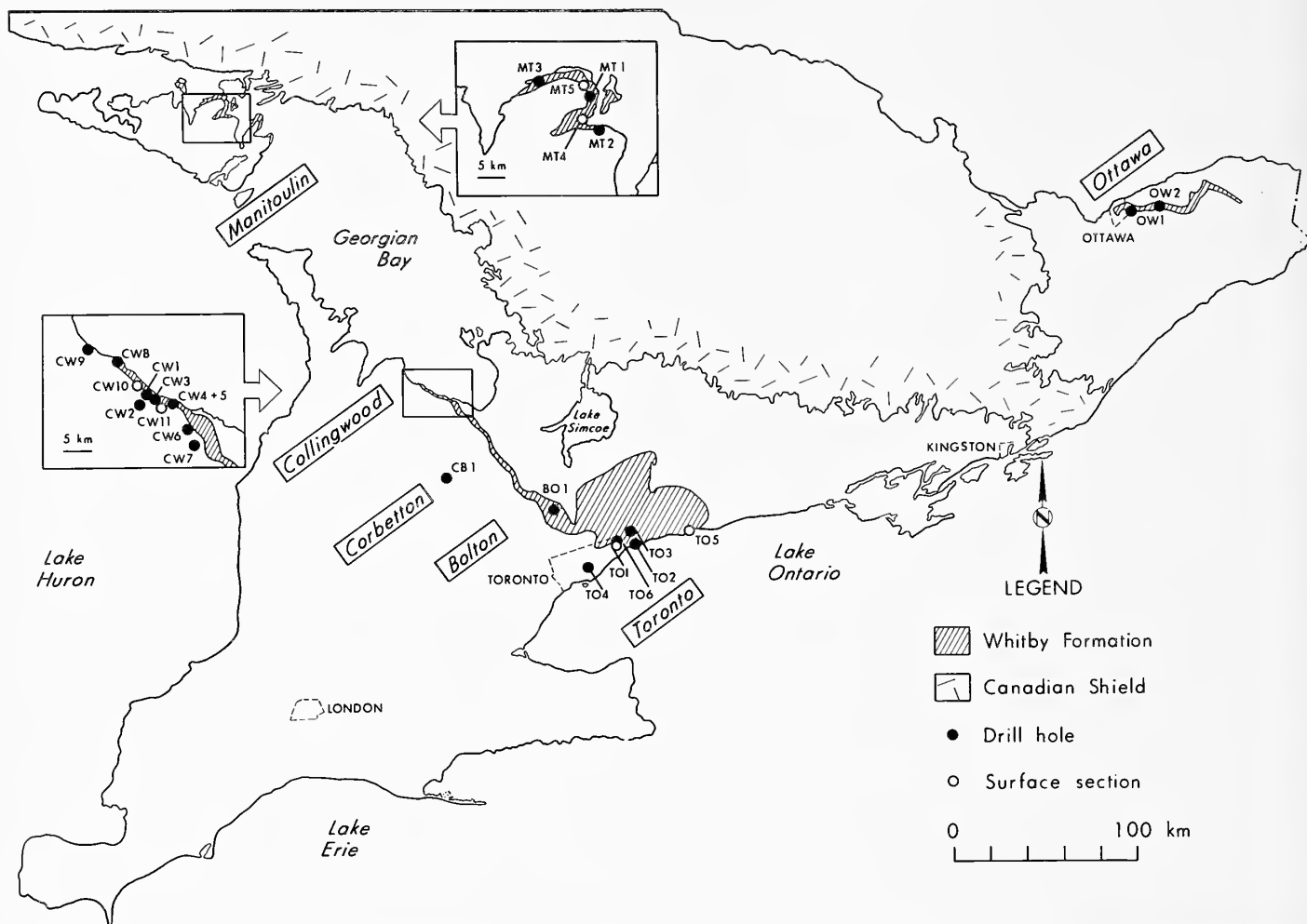


Figure 1. Locality map of southern Ontario. The map shows outcrop pattern of the Whitby Formation and the location of nineteen drill holes and six surface sections in the Ottawa, Toronto, Bolton, Corbetton, Collingwood, and Manitoulin areas.

six hundred horizons yielded single specimens of *Triarthrus*, fifty produced graptolite rhabdosomes, and another one hundred contained other shelly fossils.

Because of the small diameters of the cores, the drilling program resulted in the recovery of only a small number of specimens of *Triarthrus*: on average, a specimen every 1.5 m of strata. In order to find more specimens, short outcrop sections were measured in the Toronto, Collingwood, and Manitoulin areas. These sections yielded abundant, but stratigraphically limited, specimens. Collections of *Triarthrus* from other localities in Quebec and New York State have also been examined (Figure 2).

Stratigraphy and sedimentology of the Whitby Formation

The Whitby Formation (Liberty, 1969) is a distinctive, grey, recessive-weathering shale and siliciclastic mudstone unit that sharply overlies grey and buff nodular lime mudstones of the Cobourg Formation in southern Ontario. Its top is drawn at the first silty limestone band that defines the base of the Georgian Bay Formation (Figure 3). The Whitby

Formation increases in thickness towards the south from 25 m in the Manitoulin area to as much 90 m in the Toronto area. The fissility that characterizes most outcrops is not evident in the cores, where the Whitby consists largely of massive siliciclastic mudstones.

The Whitby Formation probably extends into the United States. A 5-7 cm veneer of bituminous shale on the Hillier Limestone at Rodman in western New York State appears to belong to this unit (Ludvigsen, 1979b, Fig. 11). Similar grey shales are assigned to the Macasty and Pointe-Bleue Formations in Quebec and to the upper Utica Shale in New York State (Figure 4).

Freshly broken surfaces of the Whitby shales vary from nearly black to light grey in color, and color remains the prime criterion for litho-stratigraphic subdivision. According to the GSA Color Chart (Goddard et al., 1980), the colors range from N3 (dark grey) to N4 (medium dark grey) to N5 (medium grey). For economy and ease of reference, these colors are herein referred to as N3 (dark grey), N4 (medium grey), and N5 (light grey).

The Whitby Formation comprises two members: a lower member of dark grey (N3) shales, and an upper member of medium and light grey (N4, N5) shales (Figure 3). The lower member consists of bituminous, fetid, variably calcareous, finely laminated and fossiliferous N3 shales

with infrequent grey limestone interbeds and thin fossil hash lags. The dark color of these shales is attributable both to a high total organic content (5-10%, in places as high as 15%; Russell and Telford, 1983, Fig. 3) in part as kerogen (Figure 5A), and to the presence of finely disseminated pyrite. This member increases in thickness from 5 m in the Manitoulin area to 10 m in the Toronto area, and to a maximum of 20 m in the Ottawa area. The lower member of the Whitby Formation as used herein corresponds to units called Utica, Collingwood, Craigeleith, Gloucester, Billings, and Eastview in earlier reports. The upper member is a monotonous sequence of silty, largely non-calcareous, and sparsely

fossiliferous N4 and N5 shales of low organic content and with few thin siltstone and bioclastic grainstone beds. The contact with the lower member is sharp to gradational over a few decimeters. The upper member increases in thickness from 20 m in the Manitoulin area to 50 m in the Collingwood and Ottawa areas, and to a maximum of 80 m in the Toronto area. The upper member as used herein corresponds to Liberty's (1969) middle and upper members of the Whitby Formation, as well as to the Rouge River, Thornbury, Blue Mountain, and Sheguindah of other authors.

The Whitby Formation has not been the subject of a systematic sedi-

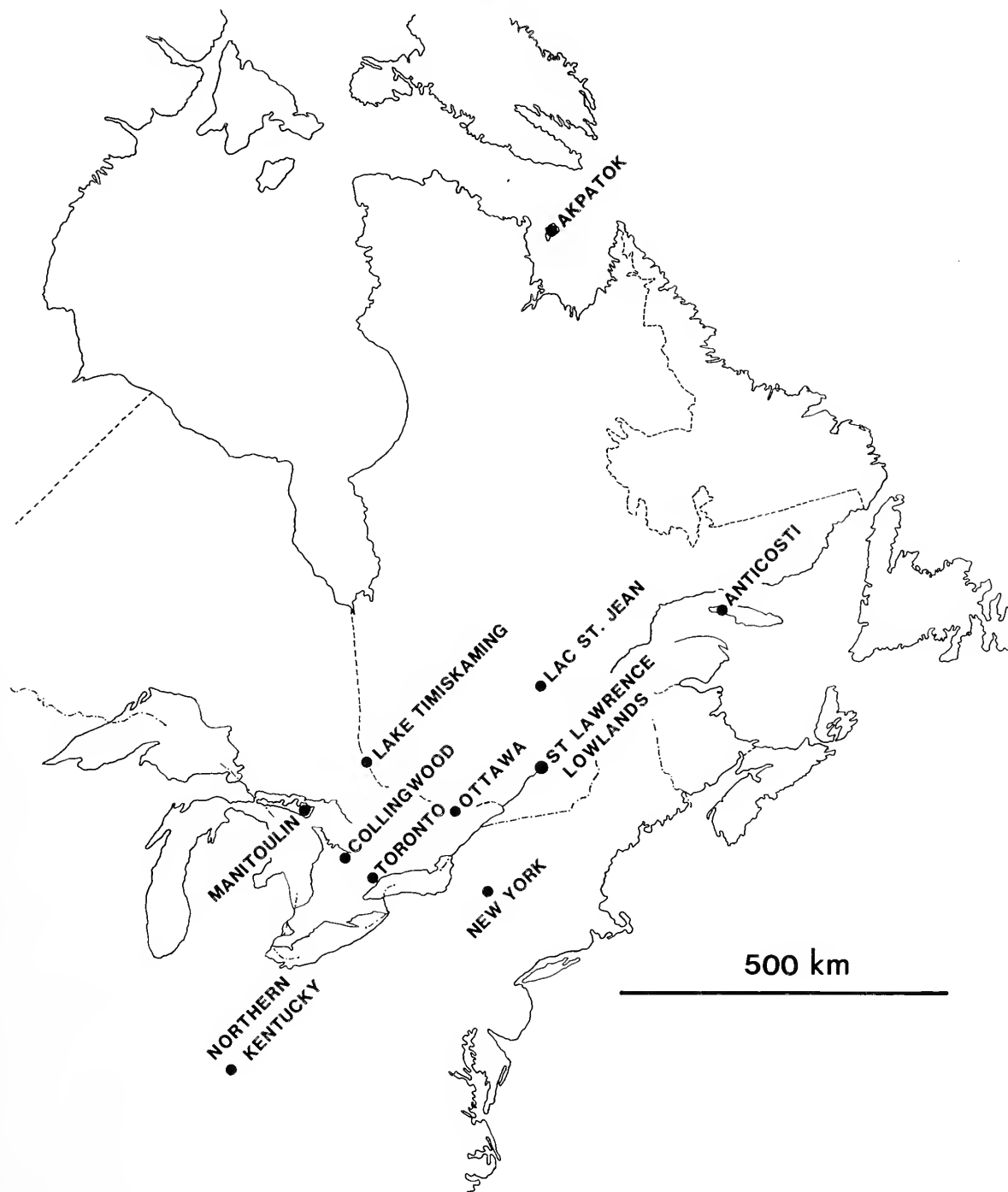


Figure 2. In North America, *Triarthrus* is largely restricted to these localities.

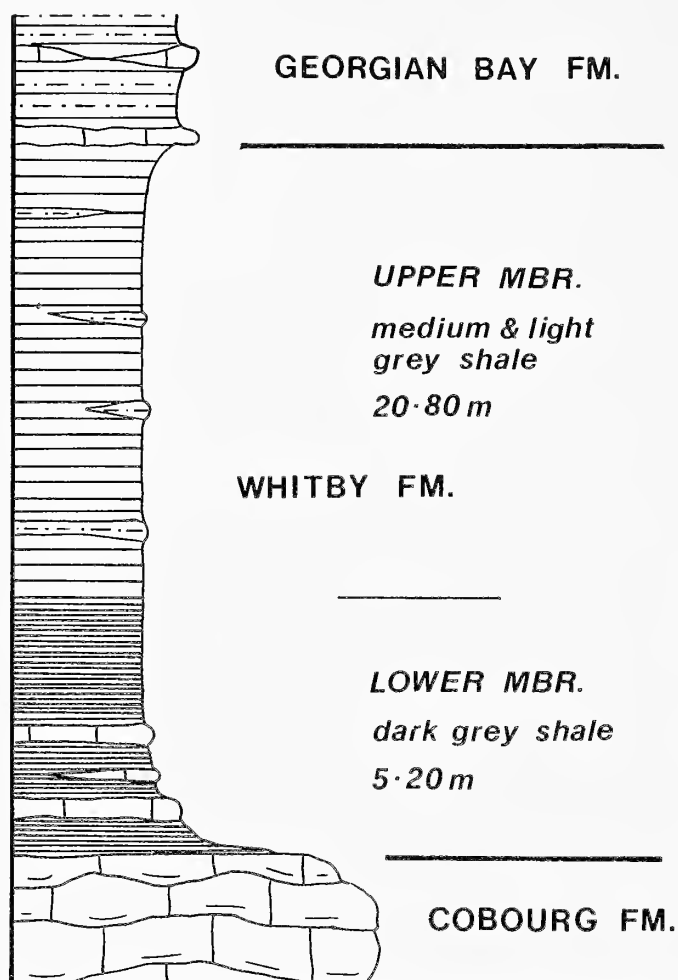


Figure 3. Composite stratigraphic section of the Whitby Formation. The entire formation does not crop out in any single locality in southern Ontario.

mentologic study. Different authors have noted that both the lithofacies and the biofacies of the lower member are strongly reminiscent of slope facies, but none has proposed a deep-water origin for these dark grey, bituminous, graptolitic epicontinental shales. Liberty (1969) suggested deposition in shallow, stagnant, non-aerated waters. Ludvigsen (1979b) proposed a moderately shallow, oxygen-poor, and cold epicontinental shelf setting for the lower member. Johnson and Rong (1989) interpreted the sharp angular unconformity at the base of the Whitby dark grey shales with Proterozoic quartzites in the Manitoulin area as the consequence of a rapid transgression across a rocky shoreline.

The presence of depositional textures that are best interpreted as tempestites supports the notion that the Whitby shales were deposited in moderately shallow water within the range of storm-wave base (see Kreisa, 1981). Common brachiopod valve lags in the lower member (Figure 5C) appear to be distal storm beds. Proximal storm beds comprise rounded phosphatized pelmicrite intraclasts above a scoured base (Figure 5B). Delicate undisturbed exuviae of *Triarthrus* (Ludvigsen, 1979a, fig. 38) and *Pseudogygites* (Ludvigsen, 1979b, fig. 3) appear to owe their preservation to quick smothering by distal mud turbidities. Graded silt laminae in the upper member (Figure 5D) may also have a tempestite origin. In addition, the grey limestone interbeds in the lower member are composed of a series of 2-5 cm-thick fining-upward

sequences, each of which has an erosional base below a bioclastic packstone that grades up into lime mudstones. These beds occur within the bituminous shales, and they are considered to be amalgamated storm beds.

The presence of tempestites within a sequence of bituminous shales is unusual, but by no means unique. Wignall (1989) recognized a variety of storm-produced beds in the bituminous Kimmeridge Clay (Jurassic) of England, and proposed a model that involved storms that mixed a thermally stratified water column and periodically supplied oxygen to anaerobic mud bottoms. As is the situation with the lower Whitby shale, the Kimmeridge Clay was deposited in an epicontinental basin well-removed from the influence of the open ocean.

For "black" shales, the lower member of the Whitby Formation is unusually fossiliferous. These bituminous shales are generally finely laminated with both pelagic elements and a fairly diverse epifauna, but entirely lack an infauna. Such characteristics imply that conditions were anaerobic below the sediment-water interface, but aerobic or dysaerobic on the sediment surface. The light and medium grey shales of the upper member are commonly bioturbated, and this part of the formation signals a return to normal aerobic conditions on and within the sediment.

Biostratigraphy of the Whitby Formation

The Whitby Formation is sparsely to abundantly fossiliferous throughout, with both benthic and pelagic elements represented. The macrofauna includes bivalves, gastropods, nautiloids, ostracodes, brachiopods, conularids, graptolites, and five genera of trilobites—*Flexicalymene*, *Isotelus*, *Pseudogygites*, *Cryptolithus*, and *Triarthrus* (see Liberty, 1969; Ludvigsen, 1979a). Earlier biostratigraphic schemes of the Whitby Formation have been based on graptolites and on *Triarthrus* because these are the only taxa that extend through the entire formation.

Graptolite biostratigraphy

John Riva of Université Laval identified graptolites from fifty levels in the Whitby cores and assigned each collection to one of two zones. Those from the lower member were assigned to a *Climacograptus pygmaeus* Zone, and those from the upper member to an *Amplexograptus manitoulinensis* Zone (see Riva, 1974). Following Bergström and Mitchell (1986), the *Climacograptus pygmaeus* Zone is herein referred to as the lower Maysvillian, and the *Amplexograptus manitoulinensis* Zone as the upper Maysvillian and lower Richmondian (Figure 4). Correlations of the Whitby Formation to other Upper Ordovician shale units in eastern North America are based primarily on graptolite biostratigraphy.

Previous biostratigraphic studies of *Triarthrus*

The distribution of different species of *Triarthrus* in Upper Ordovician shales of southern Ontario was first used for biostratigraphic purposes by Parks (1928). He established three informal zones, each restricted to a different formation:

1. A lower zone of *T. eatoni* and *Ogygites canadensis* [= *Pseudogygites latimarginatus*; see Ludvigsen, 1979b] in the upper Collingwood Formation (that is, lower Whitby Formation).
2. A middle zone of *T. glaber* [in reality, *T. canadensis*; see "Systematic paleontology"] in the lower Gloucester Formation (that is, lower upper Whitby Formation).

3. An upper zone of *T. spinosus rougensis* and *T. spinosus narrawayi* [both regarded as *T. rougensis* herein] in the upper Gloucester Formation (that is, upper Whitby Formation)

According to Parks (1928), all three formations (later united as the Whitby Formation) and all three zones are present in the Toronto and Ottawa areas, but the lower part of the Gloucester and the intermediate zone are absent in the Collingwood area. Accordingly, Parks (1928) postulated a disconformity between the upper Collingwood and the upper Gloucester in this area. Liberty (1969) and Ludvigsen (1979b, fig. 11) showed the same stratigraphic relationship as a disconformity within the Whitby Formation.

Using an approach similar to Parks' (1928), Tuffnell and Ludvigsen (1984) established three biostratigraphic units in the Whitby Formation based on frequency of occurrence of three species of *Triarthrus*: Fauna A for *T. eatoni* in the lower Whitby, Fauna B for *T. canadensis* in the lower upper Whitby, and Fauna C for *T. rougensis* in the upper Whitby.

Fisher (1977) was the only other investigator to use *Triarthrus* for detailed biostratigraphy. He showed a *Triarthrus beckii* Zone that corresponds to the *Orthograptus ruedemanni* Zone (Franklinian Stage), and a *Triarthrus eatoni* Zone for the overlying *Climacograptus spiniferus* to *Amplexograptus manitoulinensis* zonal interval in New York State (Edenian and Maysvillian stages).

A new *Triarthrus* biostratigraphy

Biostratigraphy addresses both the temporal and the spatial aspects of fossils in rock. These aspects can be brought into separate focus by manipulation of the fossil record at different taxonomic levels.

Specimen abundance of genera or families defines biofacies for spatial biostratigraphy, and presence of species defines zones for temporal biostratigraphy. Biofacies are commonly lithofacies-specific, and zones tend to be biofacies-specific (see Ludvigsen et al., 1986, for discussion).

In the Ontario–Quebec–New York area, *Triarthrus* is restricted to grey and brown shales, where it sometimes occurs in prodigious numbers, occasionally to the exclusion of other benthic elements (Ludvigsen, 1979a, figs. 38, 39A). It has not been recorded from coarse clastics or from any kind of limestone, with the exception of black argillaceous lime mudstones, and it is uncommon even in silty shales. The dominance of *Triarthrus* in the grey/brown shale lithofacies allows definition of a *Triarthrus* Biofacies that occupied slope settings in central New York during the Franklinian and Edenian (Titus and Cameron, 1976; Cisne et al., 1980) and shelf environments in Ontario and Quebec in the Maysvillian (Tuffnell and Ludvigsen, 1984; Desbiens and Lespérance, 1989; Johnson and Rong, 1989; Figure 4). The only other conspicuous trilobite components of this biofacies in Ontario are *Pseudogygites* in the lower part and *Cryptolithus* in the upper (Ludvigsen, 1979a, 1979b).

The next step in a dual biostratigraphy of *Triarthrus* in the Whitby Formation is analysis of first appearance and vertical range of each species in every drill hole through the *Triarthrus* Biofacies, in order to define species-based zones. Because the first appearance of each species is within the lowest 1 or 2% of stratal thickness of the 25-90 m-thick Whitby, it is not possible to define a conventional species-based zonation for the *Triarthrus* Biofacies. In the Whitby, *Triarthrus eatoni* first appears 13 cm above the base of the formation, *T. rougensis* 50 cm above the base, and *T. canadensis* 125 cm above the base. *Triarthrus*

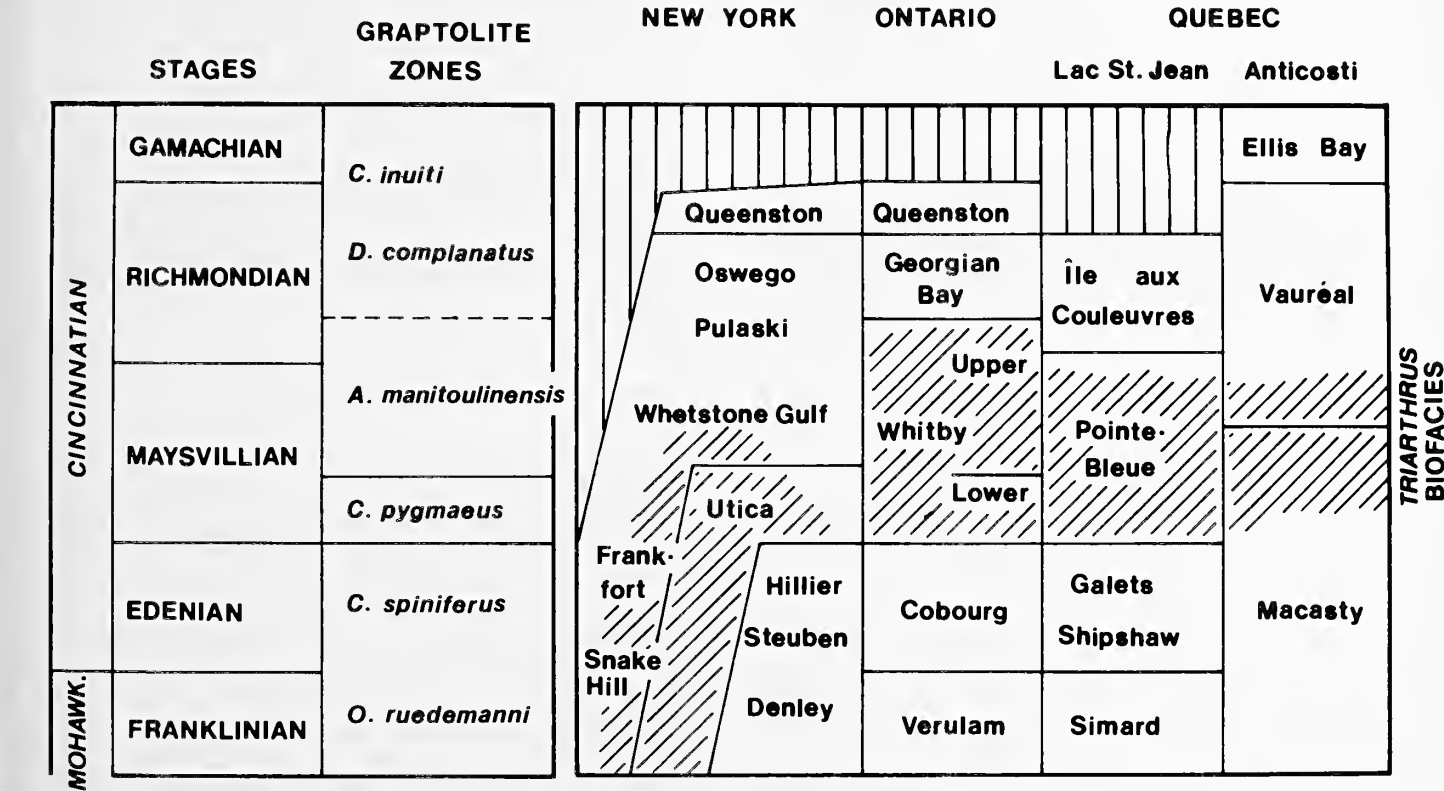


Figure 4. Correlation chart of Upper Ordovician formations in New York State, Ontario, and Quebec. A *Triarthrus* Biofacies may be mapped from upper Middle Ordovician slope facies in New York State to lower Upper Ordovician platform facies in Ontario and Quebec. The formations are largely correlated on the basis of graptolite biostratigraphy. The Franklinian Stage was defined by Sweet (1988).

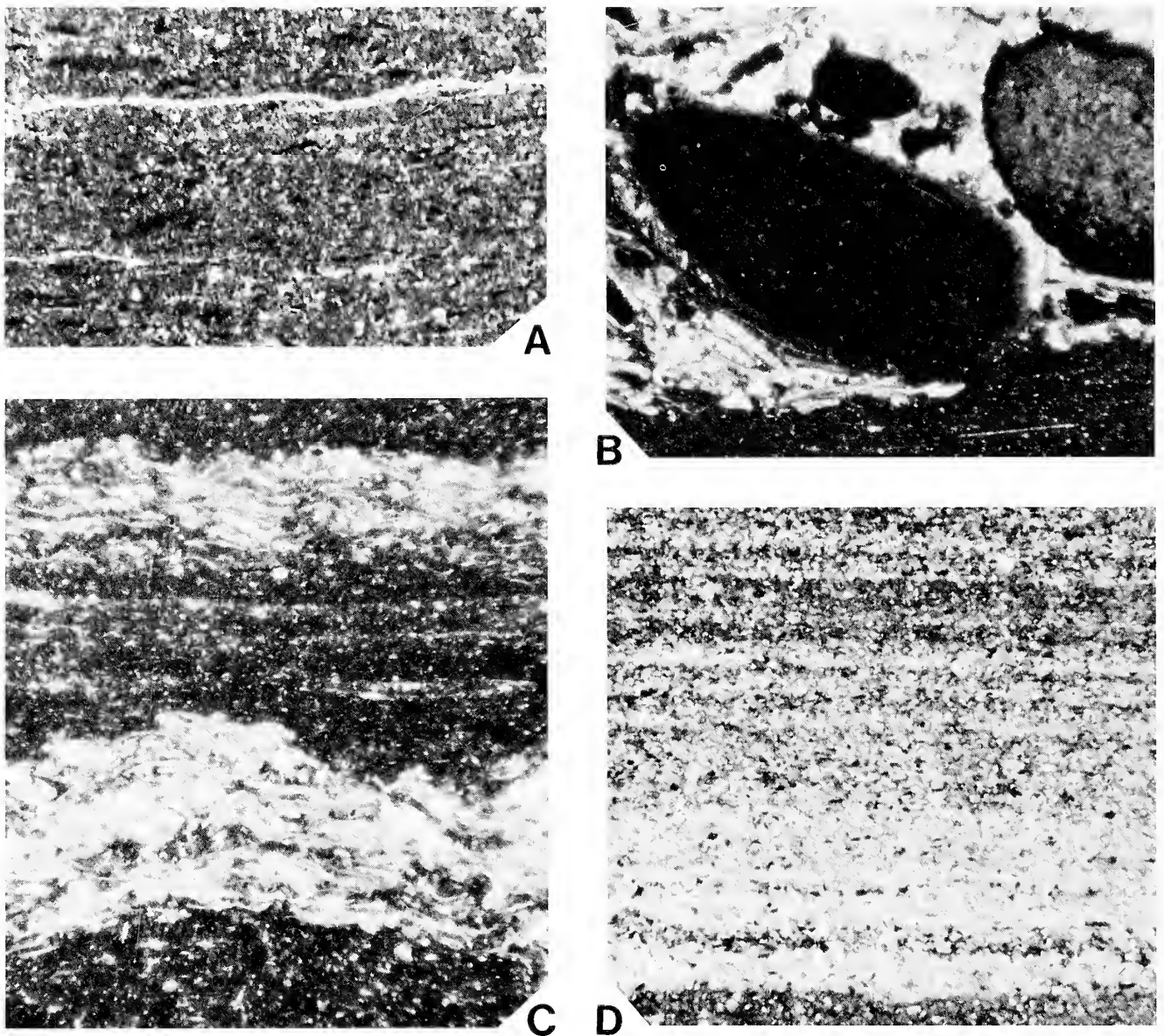


Figure 5. Thin sections of typical Whitby Formation lithologies. Width of each micrograph is 2.5 mm. *A*, Lower member. Dark grey shale with black flakes of kerogen aligned parallel to bedding. *B*, Lower member. Base of tempestite with rounded phosphatized pelmicrite intraclasts in dark grey shale. *C*, Lower member. Dark grey shale with two shell lags composed of thin brachiopod valves. *D*, Upper member. Medium grey shale with fining-upwards silt laminations.

spinosus occurs only in the Ottawa area, where it first appears 11.6 m above the base of the Whitby. Therefore, the concurrent ranges of the first three of these species frustrate any attempt to establish a species-based zonation of *Triarthrus* for the Maysvillian Stage of southern Ontario.

These distribution data lead to some obvious questions. What is the nature of the *Triarthrus* units that were called "zones" by Parks (1928) and "faunas" by Tuffnell and Ludvigsen (1984)? Are they temporal biostratigraphic units, as these authors claim? Or are they spatial biostratigraphic units defined at low taxonomic levels?

The vertical succession of different *Triarthrus* associations seems to be related to the stacking order of progressively lighter-colored shales in the Whitby Formation. That is, there appears to be a strong environmental control to the distribution of these species. In order to test the

shale color-species relationship, data were assembled on the fresh color of the shale matrix of all specimens of four species of *Triarthrus* in the Whitby cores, regardless of stratigraphic position. These data comprise six hundred and fifteen shale color-species records from nineteen drill holes.

The shale color-species correlation turns out to be unexpectedly high. Even though the four species have essentially concurrent ranges in the Whitby Formation, they rarely occur together. 100% of *Triarthrus spinosus* specimens and 92% of *T. eatoni* specimens are confined to dark grey (N3) shales, 84% of *T. canadensis* specimens to medium grey (N4) shales, and 96% of *T. rougensis* specimens to light grey (N5) shales (Figure 6). Because the dark grey shale is found in the lower part of the formation and the light grey shale in the upper part, it follows that the species associations will occur in discrete intervals that

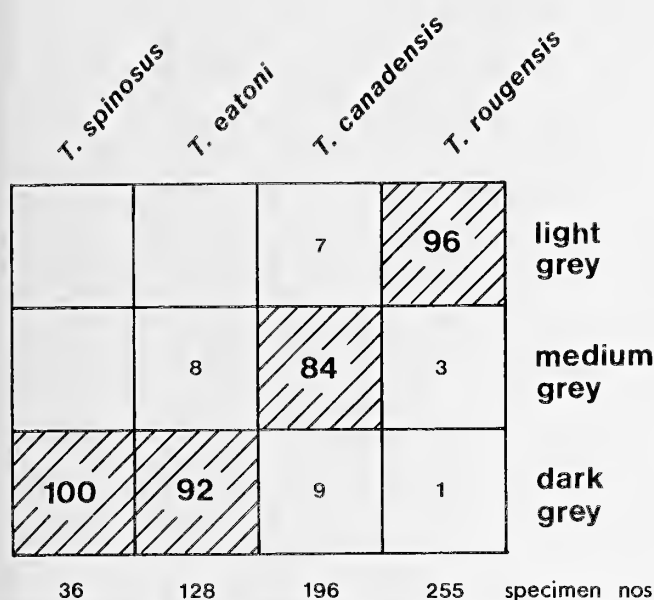


Figure 6. Species and shale colors. Even though the four species of *Triarthrus* have largely concurrent ranges in the Whitby Formation, they are rarely found together. Here, six hundred and fifteen specimens of the four species in the Whitby cores are arranged according to occurrences in three shale colors. Numbers in boxes are percentages.

stack in a regular order within the Whitby Formation—in effect, mimicking a species-based zonal succession (Figure 7). This mimicry misled both Parks (1928) and Tuffnell and Ludvigsen (1984) about the nature of the *Triarthrus* units they established. These units are not temporal biostratigraphic units as these authors thought; instead, they appear to be spatial biostratigraphic units—that is, sub-biofacies within a *Triarthrus* Biofacies. These sub-biofacies are characterized on the basis of dominance of specimens of four species: a *T. eatoni* Sub-biofacies in dark grey (N3) shales, a *T. canadensis* Sub-biofacies in medium grey (N4) shales, and a *T. rougensis* Sub-biofacies in light grey (N5) shales (Figure 8). These diachronous sub-biofacies are mappable from the Collingwood area of southern Ontario to Anticosti Island (Figure 9).

Decline and demise of *Triarthrus*

The Olenidae was one of more than a dozen trilobite families that became extinct near the top of the Ordovician. The Agnostidae, Asaphidae, Cyclopygidae, Nileidae, Remopleuridae, Telephinidae, Trinucleidae, and Pterygometopidae, among others, also became extinct in this interval. In searching for some commonality in the life habits of these morphologically disparate groups to help explain their nearly concurrent extinction, Fortey (1989, p. 345) concluded that “nearly all of the trilobites were deeper-shelf forms, or had a phase in their life cycle as part of the oceanic plankton.” He suggested that the extinctions were part of a global oceanic crisis predicated by the terminal Ordovician glaciation (see also Sheehan, 1988). The Olenidae, represented solely by *Triarthrus*, the last olenacean, is in many ways significantly different from the other families destined for extinction near the top of the Ordovician. Unlike the other taxa that were exterminated in the Gamachian or Hirnantian, *Triarthrus* became extinct earli-

er, in the early Richmondian (a correlative with the Cautleyan or, possibly, the Rawtheyan Stage of Britain). It should be noted that Owen’s (1987) extension of the range of *Triarthrus* into the Hirnantian is in error. In addition, there is no evidence that *Triarthrus* was ever part of the plankton; both larvae and adults had a benthic life mode (Chatterton and Speyer, 1989). Indeed, at the time of its extinction, this trilobite was an inhabitant of shallow shelf settings well-removed from the open ocean. Finally, unlike the other families, which were widely distributed at the time of their extinction in the Late Ordovician, the Olenidae was largely restricted to a single area in eastern North America.

It is here suggested that both the Maysvillian flowering of *Triarthrus* in New York, Ontario, and Quebec and its extinction a few million years later are attributable to a local cause—the Taconian Orogeny. Consequences of global environmental crises that accompanied the waxing and waning of Late Ordovician ice sheets are not explicitly dealt with, largely because the sedimentologic response of factors such as sea-level drop, oceanic cooling, oceanic overturn, and widespread anoxia (see Fortey, 1989; Sheehan, 1988) cannot readily be differentiated from the sedimentologic response to local tectonic events. Our preference is to emphasize a well-documented local cause instead of a number of complex global causes. Accordingly, the extinction scenario outlined below does not address the Late Ordovician demise of one or two species of *Triarthrus* in northern Europe and China.

The majority of North American localities with *Triarthrus* are in a broad belt of Maysvillian shales that extends from southern Ontario and New York across southern Quebec to Anticosti Island (Figure 2). This apron of *Triarthrus*-bearing shales is located immediately in front of the late Middle Ordovician overthrusts in the New England and eastern Quebec areas. The proximity is not fortuitous.

Rowley and Kidd (1981, Fig. 4) and Cisne et al. (1982) summarized the evidence that the Taconian Orogeny in the New England area represented a volcanic arc–continent collision in the latest Middle Ordovician. Quinlan and Beaumont (1984) suggested that successive foreland basins in eastern North America developed in response to loading of overthrusts in the adjacent Taconian Orogen. The overthrusts depressed the lithosphere as a foreland basin, and they served as sources of the clastic sediment that eventually filled the basin (Figure 10). Because the phases of the Taconian Orogeny seem to exert primary control on the distribution of the lithofacies-specific *Triarthrus* Biofacies, a tectonic model is proposed herein to explain the modest Late Ordovician radiation of *Triarthrus* in North America and its extinction a few million years later (Figure 11).

During the Franklinian and Edenian (Figure 11A), the deep graptolitic Taconic Trough in eastern New York State was rapidly being filled with turbiditic sediments. These were derived from the rising Taconian Orogen, which had formed from imbricate thrust sheets that had been advancing westward during the Middle Ordovician until a climax phase in the late Franklinian (*Orthograptus ruedemanni* Zone; see St. Julien and Hubert, 1975, p. 352; Rowley and Kidd, 1981, p. 214). Cratonwards of this trough were shallow-water carbonate sands and muds of a broad Trenton Shelf that extended from Michigan to Quebec and from New York to Manitoulin Island and beyond. At this time, the *Triarthrus* Biofacies was confined to dark grey shales on the flank(s) of the Taconic Trough; this was essentially the traditional position occupied by the oleniid biofacies along the edge of platforms (Fortey, 1975; Ludvigsen and Westrop, 1983a).

In the earliest Maysvillian (Figure 11B), lithospheric downwarp of the Trenton Shelf in response to loading of Taconian thrust sheets creat-

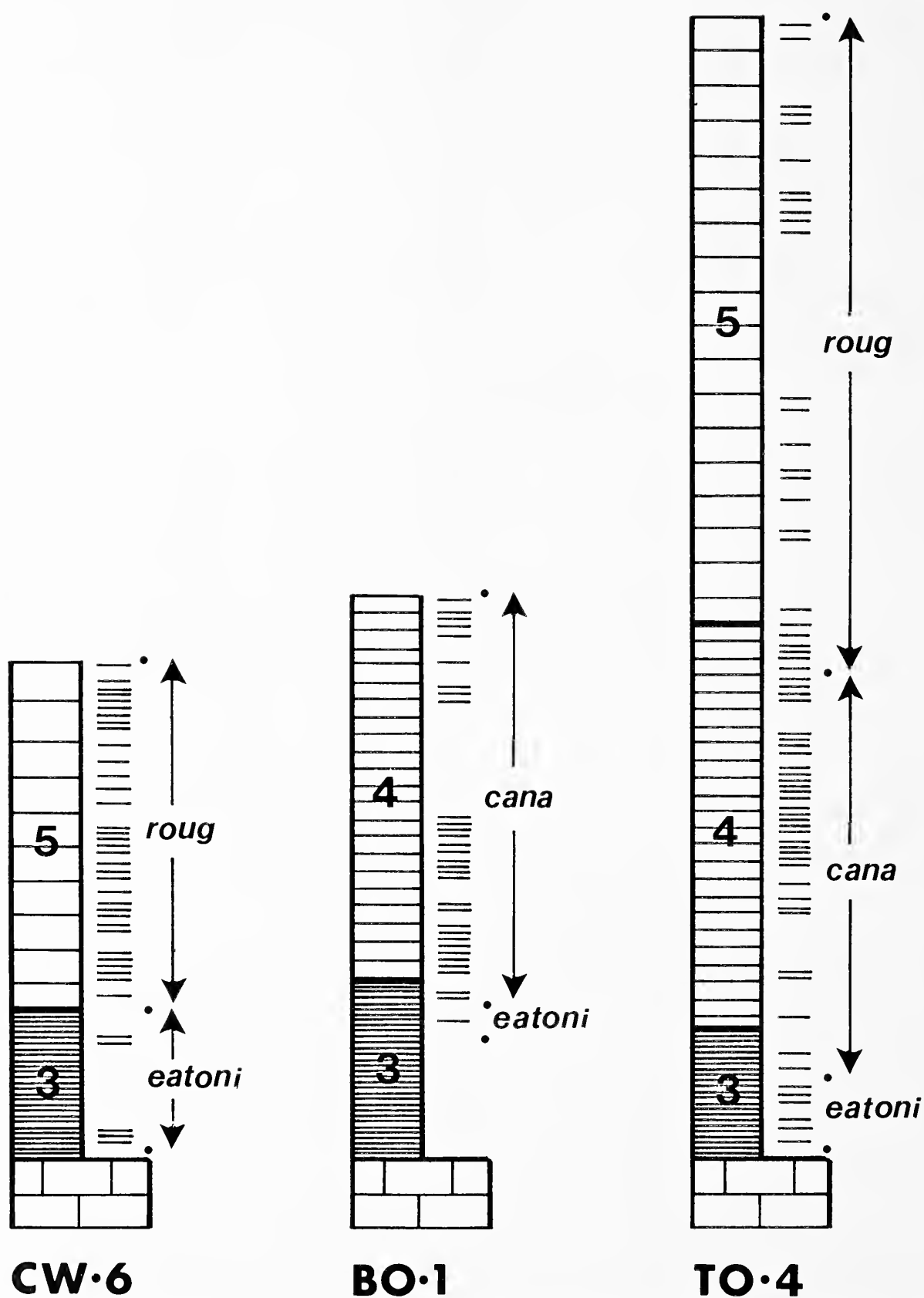


Figure 7. The Whitby shales become lighter-colored upsection. Three representative drill holes are shown: forty-five *Triarthrus*-bearing horizons in CW-6, forty-five in BO-1, and ninety-six in TO-4. The *T. eatoni*, *T. canadensis*, and *T. rougensis* intervals correspond closely to the N3, N4, and N5 shale colors, respectively.

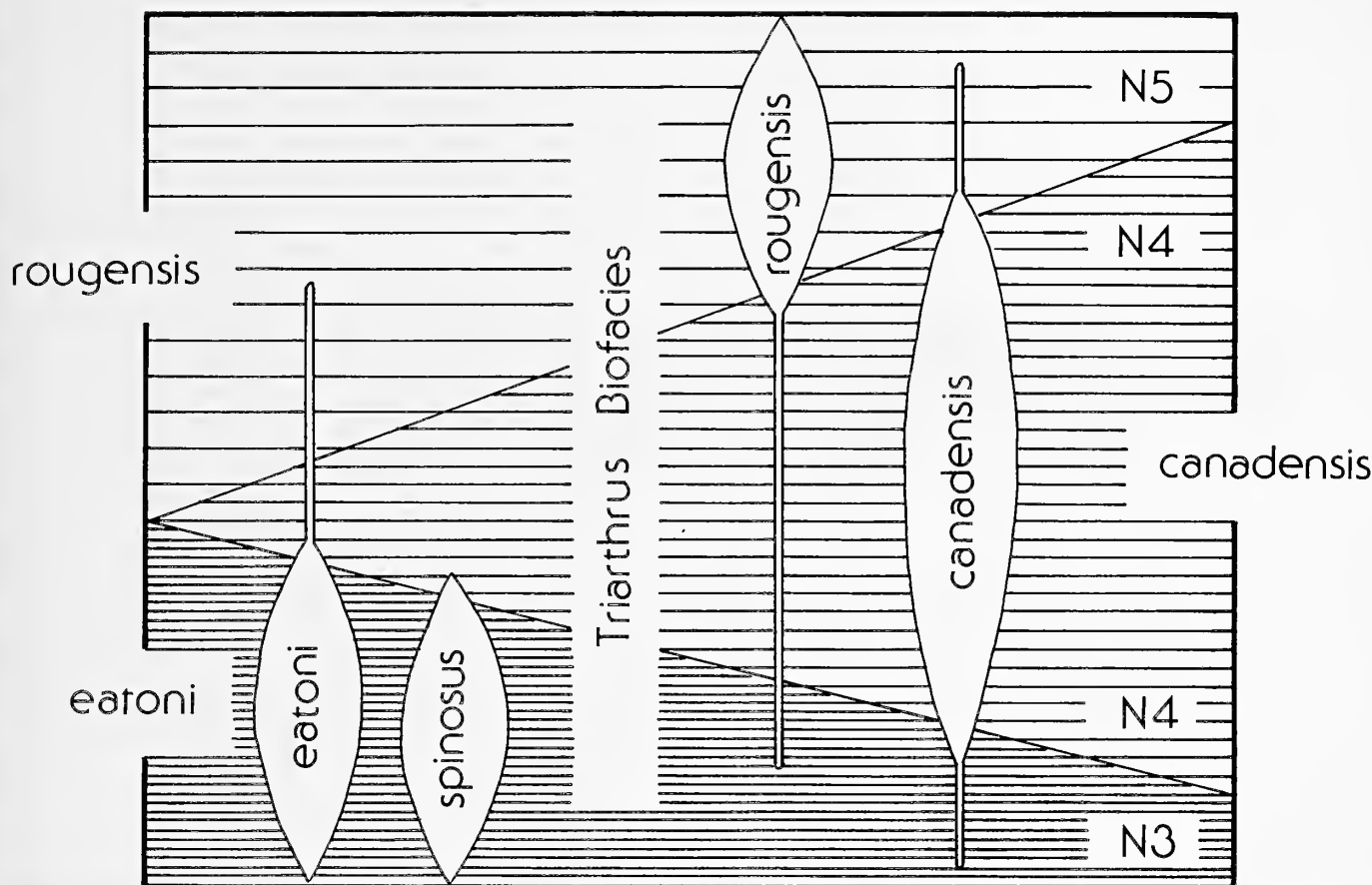


Figure 8. Relationship of sub-biofacies and shale colors. *Triarthrus* Biofacies in the Whitby Formation comprises three sub-biofacies established on the basis of relative abundance of four species of *Triarthrus*: a *T. eatoni* Sub-biofacies in dark grey (N3) shale, a *T. canadensis* Sub-biofacies in medium grey (N4) shale, and a *T. rougensis* Sub-biofacies in light grey (N5) shale.

ed a new epicratonic basin, herein named the "Utica Basin" (Figure 10). This downwarp terminated carbonate deposition synchronously across the entire 150,000 km² basin. At about the same time, the Taconic Arc rose above sea level as the continental crust was being subducted, and as a result increasing volumes of coarse clastic sediment were shed cratonward, eventually to fill the Taconic Trough. With the removal of the trough as a sediment trap, fine-grained sediment could now sweep unimpeded into the Utica Basin. Initially, this sediment comprised organic-rich muds deposited under reducing conditions across the entire basin. These dark grey muds were replaced by medium grey and light grey muds as progressive ventilation accompanied increases in sediment supply.

The *Triarthrus* Biofacies tracked the lithofacies that shifted in response to the climax phase of the Taconian Orogeny. Evicted from its previous slope position when the Taconic Trough became filled during the Edenian, the *Triarthrus* Biofacies moved to a new setting as organic-rich muds were deposited across the entire Utica Basin. It is likely that the Maysvillian diversification of *Triarthrus* was a direct response to the availability of new muddy habitats on the craton. The *T. eatoni* Sub-biofacies became established in the dark grey, reducing, organic-rich muds that flooded the entire basin. Somewhat later, as sediment influx increased and the organic content of the muds decreased, it was replaced by the *T. canadensis* Sub-biofacies in medium grey muds and, later still, by the *T. rougensis* Sub-biofacies in light grey muds.

By the late Maysvillian, both the dark and medium grey muds had disappeared from the now much-smaller Utica Basin (Figure 11C), with the attendant loss of both the *T. eatoni* and *T. canadensis* Sub-biofacies and their constituent species. Light grey muds of the *T. rougensis* Sub-biofacies remained, but only for a short time, before these too were obliterated by the prograding coarse clastics of the Queenston Delta, which terminated deposition in the Utica Basin (Figure 11D). The demise of the *T. rougensis* Sub-biofacies in the early Richmondian marked the extinction of *T. rougensis*, the last olenacean trilobite species.

In summary, the Maysvillian diversification of *Triarthrus* in North America took place within the Utica Basin, a short-lived foreland basin of the Taconian Orogeny. Ironically, later phases of the same orogeny caused extinction of this stenotopic trilobite by destruction of its sole habitat.

Systematic paleontology

Repositories.—Illustrated specimens of *Triarthrus* are deposited at the Royal Ontario Museum, Toronto (ROM); the New York State Museum, Albany (NYSM); the United States National Museum of Natural History, Washington (USNM); and the Yale Peabody Museum of Natural History, New Haven (YPM).

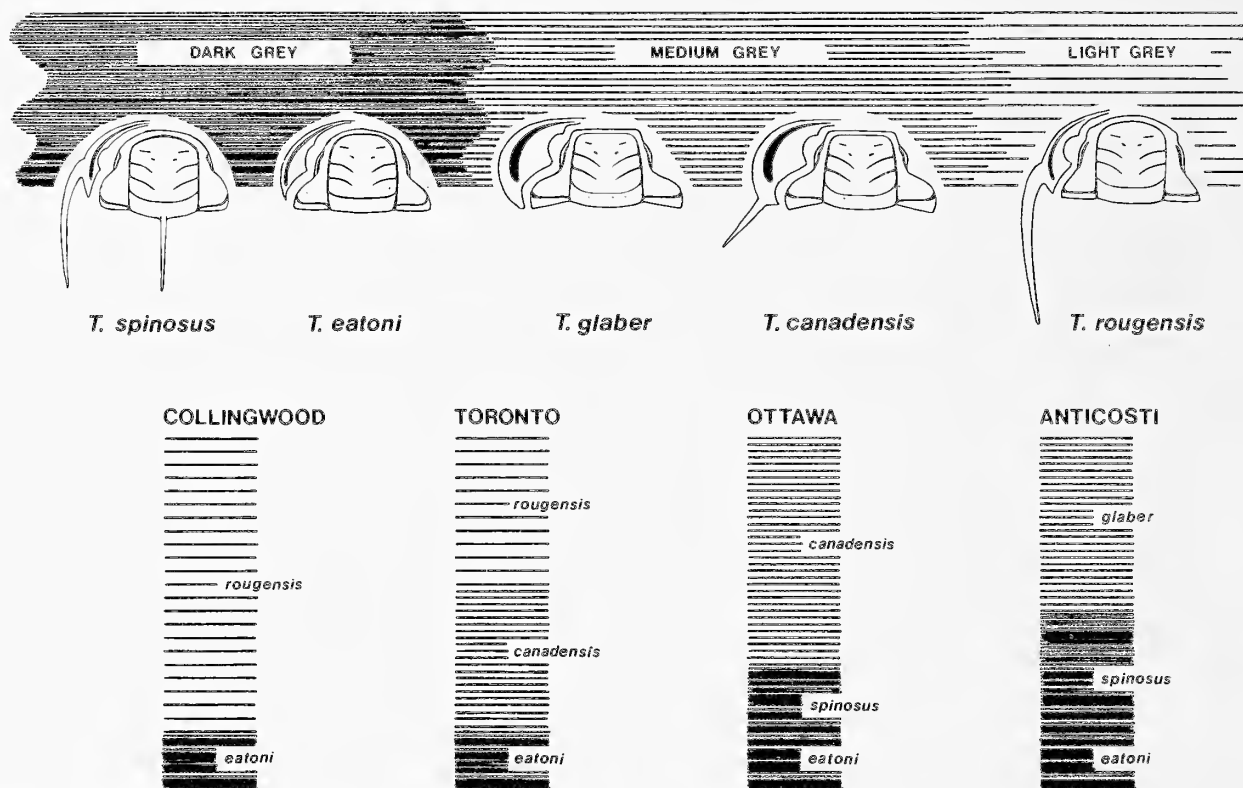


Figure 9. The three sub-biofacies are mappable from southern Ontario to Anticosti Island.

Subclass LIBRISTOMA Fortey, 1990

Order PTYCHOPARIIDA Swinnerton

Superfamily OLENACEA Burmeister

Family OLENIDAE Burmeister

Subfamily TRIARTHURINAE Ulrich, 1930 [=BALNIBARBIINAE Fortey]

Diagnosis.—Olenids with a broad, quadrate glabella bearing four pairs of simple lateral furrows; 1S and 2S curve slightly backwards from axial furrows; 3S and 4S are isolated. Palpebral lobes are located close to glabella. Two pleural furrows, a backwardly curving anterior pleural furrow and a transverse or forwardly curving posterior pleural furrow, extend out from axial furrow.

Assigned genera.—*Triarthrus* (*Triarthrus*) Green, 1832; *Triarthrus* (*Danarcus*) n. subgen.; *Bienvillia* Clark, 1924; *Westergaardites* Troedsson, 1937; *Porterfeldia* Cooper, 1953; *Leiobienvillia* Rasetti, 1954; *Balnibarbi* Fortey, 1974; and *Cloacaspis* Fortey, 1974.

Age.—Late Cambrian to Late Ordovician (Sunwaptan to Maysvillian or early Richmondian in North America).

Remarks.—Fortey (1974) drew attention to the diagnostic value of

the number and arrangement of pleural furrows as a means of differentiating olenid subfamilies. Because *Triarthrus* and allied genera bear two pleural furrows on each thoracic segment—a posterior furrow and an anterior furrow (Figure 12)—earlier synonymy of the Triarthrinae with the Oleninae (Ludvigsen, 1982, p. 55; Ludvigsen and Tuffnell, 1983, p. 571; see also Henningsmoen, 1957, p. 96) is now rejected. Olenines such as *Olenus* and *Parabolinella* bear only a single pleural furrow; they lack the posterior pleural furrow (see Rushton, 1983, Pl. 17, fig. 4; Ludvigsen, 1982, fig. 49 I). In addition, they have a narrower axis than triarthrines and a forwardly narrowing glabella.

The Balnibarbiinae was established by Fortey (1974) for Lower Ordovician triarthrine-like olenids that possess an apparently unique morphological feature—a triangular “pleural node” outlined, according to Fortey (p. 14, fig. 4), by the forked pleural furrow and by the axial furrow. However, if this furrow arrangement is described as the juncture of two pleural furrows instead of the splitting of a single pleural furrow, it is clear that two furrows cross the inner part of the pleurae of both *Balnibarbi* and *Triarthrus*. In the former genus they meet; in the latter they do not. This is the only difference. Accordingly, the pleural furrow

arrangement of these genera is essentially identical and, therefore, the Balnibarbiinae is considered a junior synonym of the Triarthrinae.

Genus TRIARTHURUS Green, 1832

Type species.—*Triarthrus beckii* Green, 1832, from the Snake Hill Formation at Cohoes Falls, New York State (by monotypy).

Diagnosis.—A genus of Triarthrinae with a short and convex frontal area. Cephalic border furrow does not cross anterior facial suture, but instead dies out in front of the axial furrow, or passes in front of the suture. Palpebral lobes are located anterior of glabellar midlength. Thorax of twelve to fourteen segments.

Remarks.—The large number of Lower, Middle, and Upper Ordovician species previously assigned to *Triarthrus* was, on the basis of frontal area morphology, reduced to ten Upper Ordovician species by Ludvigsen and Tuffnell (1983, p. 571). These species are here assigned either to *Triarthrus* (*Triarthrus*) or to *Triarthrus* (*Danarcus*) n. subgen. Remaining Lower and Middle Ordovician species belong either to *Porterfieldia* or *Bienvillia*. *Triarthrus* differs from all other triarthrines in that the cephalic border furrow does not cross the anterior facial suture, but instead remains in front of this suture for its entire course (Ludvigsen and Tuffnell, 1983, fig. 1).

Virtually all known specimens of *Triarthrus* are flattened in shale. The unique enrolled specimens of *T. (T.) beckii* from the lower Kope Formation (Edenian) of Kentucky illustrated by Ross (1979, Pl. 1, figs.

1-13) demonstrate unequivocally that this species originally possessed a moderately convex cephalon with a broad anterior arch. Other species of *T. (Triarthrus)* probably possessed comparable degrees of inflation. *T. (Danarcus) glaber* is represented entirely by flattened specimens, but this species probably possessed a highly vaulted cephalon based on the size of the anterior arch.

The two subgenera of *Triarthrus* are distinguished on the basis of width of free cheek, shape of preglabellar furrow, shape of cephalon, width of anterior cephalic arch, and shape of glabella. They possess clearly distinguishable pygidia. *Triarthrus* (*Triarthrus*) has a small pygidium with four axial rings and lacks a border. The pygidium of *T. (Danarcus)* is larger, with five axial rings and a conspicuous convex border. The species of both subgenera are differentiated on the basis of presence and size of genal spines, presence of median spine(s) on thorax, size and location of palpebral lobe, and presence of an occipital spine.

Triarthrus hypostomes consist of small, thin, flat shields that are preserved only rarely. Sparse material from the Whitby Formation now suggests that each subgenus had a distinct hypostome. Hypostomes of *T. (Triarthrus) eatoni* and *T. (T.) rougensis* have narrow borders, an undifferentiated central body, and a transverse front margin (see also Whittington, 1988, Fig. 2). In life, these hypostomes would have been horizontally oriented and would have paralleled the dorsal plane of the cranium. By contrast, the hypostome of *T. (Danarcus) canadensis* is

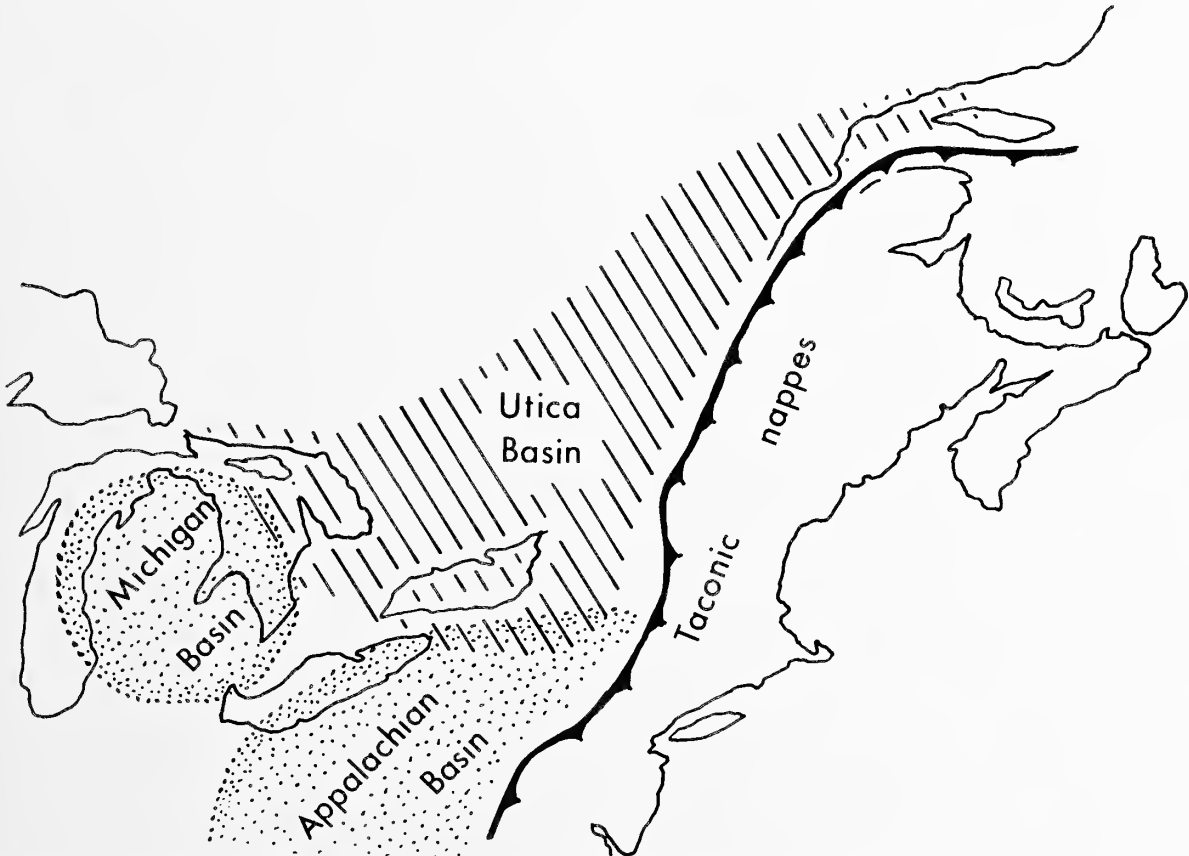


Figure 10. The Utica Basin. This basin (defined herein) was a short-lived foreland basin formed during the Maysvillian by lithospheric downwarp in response to loading of overthrusts in the adjacent Taconian Orogen. The basin was floored by dark grey bituminous shales.

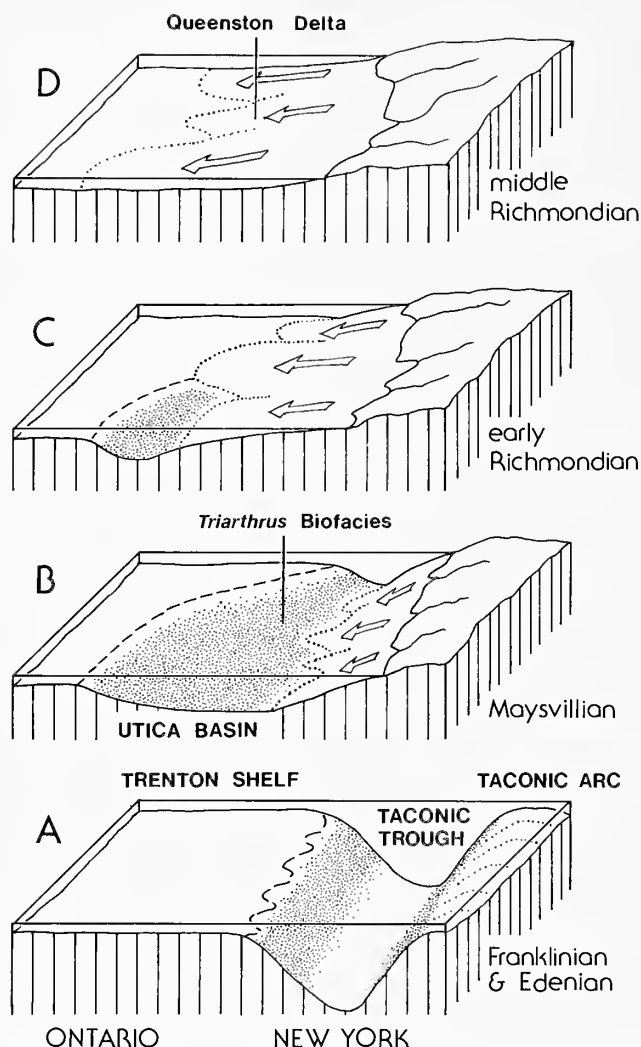


Figure 11. The distribution and disappearance of the *Triarthrus* Biofacies (fine stipple) in the New York-Ontario area was directly controlled by phases of the Taconian Orogeny. **A**, During the Franklinian-Edenian, the *Triarthrus* Biofacies occupied slope settings off the Trenton carbonate shelf. The Taconic Trough served as a sediment trap for turbidities that were swept off the rising Taconic Arc. **B**, In the early Maysvillian, lithospheric downwarp of the shelf in response to tectonic loading of Taconian overthrusts created the Utica Basin. The *Triarthrus* Biofacies shifted to the muds in this epicratonic foreland basin as coarse siliciclastics from the now-emergent Taconic Arc filled the Taconic Trough. **C**, By the early Richmondian, coarse siliciclastics of the Queenston Delta (open arrows) had prograded across most of the Utica Basin, and the *Triarthrus* Biofacies was now much-reduced in extent. **D**, By the middle Richmondian, the Utica Basin had been filled completely by coarse siliciclastics. The *Triarthrus* Biofacies had been eliminated, and *Triarthrus* was exterminated.

significantly larger, the borders carry conspicuous terrace lines, the central body bears a pair of raised elongate oval areas composed of thin shell material, and the front margin is forwardly bowed. This hypostome was probably obliquely oriented beneath the front part of the cephalon within the high anterior cephalic arch.

The speculative phylogeny of North American species of *Triarthrus* (Figure 13) shows that two species of *T. (Triarthrus)* and two species of *T. (Danarcus)* were derived from *T. (T.) eatoni* during the earliest Maysvillian.

Subgenus TRIARTHURUS (TRIARTHURUS) Green, 1832

Diagnosis.—A subgenus of *Triarthrus* with a gently arched semicircular cephalon, a parallel-sided or barrel-shaped glabella that is anteriorly rounded, narrow free cheeks, and a small pygidium without a border.

Species assigned.—Four species from eastern North America [*Triarthrus (Triarthrus) beckii* Green, 1832; *T. (T.) eatoni* (Hall, 1838); *T. (T.) spinosus* Billings, 1857; and *T. (T.) rougensis* Parks, 1921]. One species each from northern Europe [*T. (T.) linnarssoni* Thorslund, 1940] and southwest China [*T. (T.) sichuensis* Lu and Chang, 1974].

Triarthrus? billingsi Barrande, 1872, is known from a unique and somewhat deformed specimen with sixteen thoracic segments from an unknown horizon at Cap Tourmente, Quebec (Ludvigsen and Tuffnell, 1983, Pl. 3, fig. 3). This species could belong to either *Triarthrus* or *Porterfieldia* Cooper. It is not considered further in this report.

Age.—Franklinian to Maysvillian or early Richmondian in eastern North America. Early Ashgillian in northern Europe and southwest China.

TRIARTHURUS (TRIARTHURUS) BECKII Green, 1832

Plate 1, figures A, B; Figure 14

Triarthrus Beckii GREEN, 1832, p. 87, Pl. 1, fig. 6.

Paradoxides Beckii (Green). HALL, 1838, p. 142, fig. 1.

Calymene beckii (Green). HALL, 1847, p. 237, Pl. 66, figs. 2f, g [not Pl. 64, figs. 2b, c, Pl. 66, figs. 2a, b, d, e, =*T. (T.) eatoni*].

Triarthrus beckii Green. LOGAN, 1863, fig. 200; RUEDEMANN, 1926, p. 115, Pl. 21, figs. 10-12.

Triarthrus eatoni (Hall). WHITTINGTON, 1957, p. 941, Pl. 116, figs. 1-13; ROSS, 1979, p. 2, Pl. 1, figs. 1-13.

Triarthrus beckii Green. LUDVIGSEN AND TUFFNELL, 1983, Pl. 1, fig. 1; TUFFNELL AND LUDVIGSEN, 1984, p. 6j, Pl. 1, figs. 1, 2. [not *Triarthrus beckii* Green.] RAYMOND, 1920, Pls. 1-6 [= *T. (T.) eatoni*]; FOERSTE, 1924, p. 239, Pl. 43, fig. 22 [= *T. (T.) eatoni*].

Diagnosis.—A species of *Triarthrus (Triarthrus)* with short palpebral lobes located opposite 3P lobes, a barrel-shaped glabella, and rounded genal corners.

Types.—Green's (1832) original types of *T. beckii* have been lost for many years. Fortunately, Green distributed plaster casts of the type slab to a number of institutions and individuals, and some of these casts are still extant. A specimen from the U.S. National Museum of Natural History is illustrated herein (Plate 1, figure A; USNM 4966). This slab came from "black shaly limestone on the canal near Cohoes Falls," which, according to Ruedemann (1926, p. 115), is within the Snake Hill Formation, a silty equivalent of the Utica Shale (Fisher, 1977, Pl. 4).

Occurrences.—Snake Hill Formation, Dolgeville Formation, and Utica Shale (Franklinian to lower Maysvillian) of New York State (Ruedemann, 1926; Whittington, 1957). Kope Formation (Edenian) of Kentucky (Ross, 1979).

Remarks.—*Triarthrus (Triarthrus) beckii* is most similar to *T. (T.) eatoni*, and the two species have been considered synonymous by most investigators ever since the synonymy was first suggested by Hall (1847). Ruedemann (1926, p. 116), however, recognized that consistent differences in glabellar shape and in the length and position of palpebral lobes require that two distinct species be recognized. Cisne et alii's (1980) synonymy of the two species was based on multivariate analysis of six linear and six angular measurements of crania from the Franklinian part of the Dolgeville Formation of New York (a transitional facies between the Denley Limestone and the Utica Shale; Figure 4). Because none of Cisne et alii's (1980) measurements quantified the size and position of the palpebral lobe (the

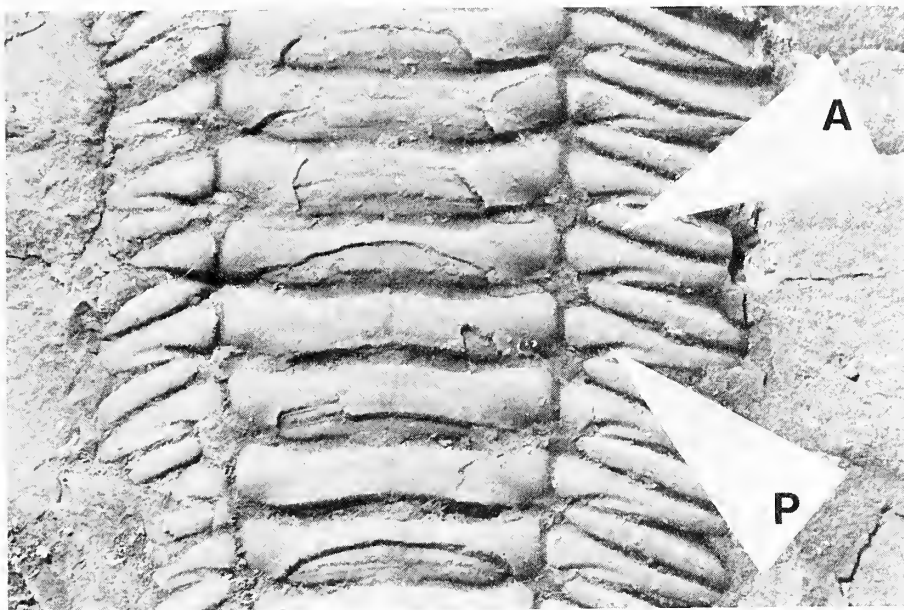


Figure 12. The presence of two pleural furrows on each segment is a key autapomorphy for the Subfamily Triarthrinae. The central part of the thorax of *Triarthrus* (*Triarthrus*) *eatoni* from the Utica Shale near Fort Plain, New York State (USNM 23587, x4.5), is shown (A is anterior pleural furrow; a is posterior pleural furrow).

prime criterion that distinguishes *T. beckii* from *T. eatoni*), their taxonomic conclusions are not convincing. Both the “*beckii*” morph and the “*eatoni*” morph shown in their Figure 2 have short, anteriorly located palpebral lobes and therefore belong to *T. (T.) beckii*. It is probable that none of the cranidia quantified by Cisne et alii (1980) belongs to *T. (T.) eatoni*.

In glabellar outline and in size and position of palpebral lobes, cranidia of *Triarthrus* (*T.*) *linnarssoni* Thorslund [= *T. skutensis* Thorslund; see Owen, 1981] from the lower Ashgillian of Norway and Sweden are identical to those of *T. (T.) beckii* (compare Plate 1, figure B of this report, with Thorslund, 1940, Pl. 12, fig. 4). Were it not for the presence of long slender genal spines in the Scandinavian form, the two species would have been synonymized herein.

TRIARTHURUS (TRIARTHURUS) EATONI (Hall, 1838)

Plate 1, Figures C-J, Plate 3, figure H; Figure 15

Paradoxides eatoni HALL, 1838, p. 142, Fig. 2.

Calymene beckii (Green). HALL, 1847, p. 237, Pl. 64, figs. 2b, c, Pl. 66, figs. 2a, b, d, e.

Triarthrus beckii var. *macastyensis* TWENHOFEL, 1914, p. 35; TWENHOFEL, 1927, p. 324, Pl. 55, fig. 6.

Triarthrus beckii Green. RAYMOND, 1920, p. 39, Pls. 1-6; FOERSTE, 1924, p. 240, Pl. 43, fig. 22.

Triarthrus eatoni (Hall). RUEDEMANN, 1926, p. 119, Pl. 21, figs. 7-9; KAY, 1937, Pl. 10, unnumbered fig.; CISNE, 1975, Pls. 1, 2; LUDVIGSEN, 1978, Pl. 6, fig. 54; LUDVIGSEN, 1979a, Figs. 12, 38, 39a, b; VERMA, 1979, photo 3, Pl. 1, figs. 1, 2; CISNE, 1981, Pls. 17-23; LUDVIGSEN AND TUFFNELL, 1983, Pl. 1, fig. 5, Pl. 2, figs. 6-8j, Pl. 3, figs. 1, 2; TUFFNELL AND LUDVIGSEN, 1984, p. 10, Pl. 1, figs. 3-6, Pl. 2, figs. 1-4; WHITTINGTON AND ALMOND, 1987, p. 7, Pls. 1-10; DESBIENS AND LESPÉRANCE, 1989, fig. 3A, B.

Triarthrus huguesensis Foerste. RUEDEMANN, 1926, p. 123, Pl. 20, figs. 5, 6.

Triarthrus macastyensis Twenhofel. BOLTON, 1970, Pl. 6, fig. 8.

not *Triarthrus eatoni* (Hall), WHITTINGTON, 1957, p. 941, Pl. 116,

TRIARTHURUS DANARCUS

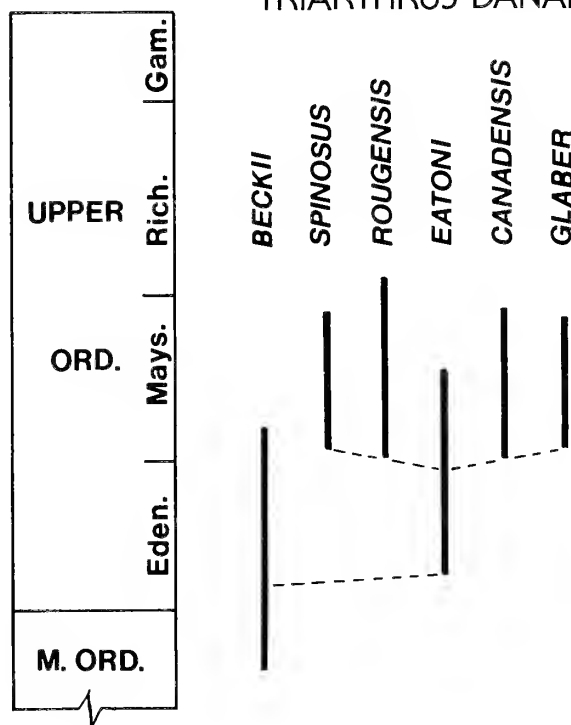
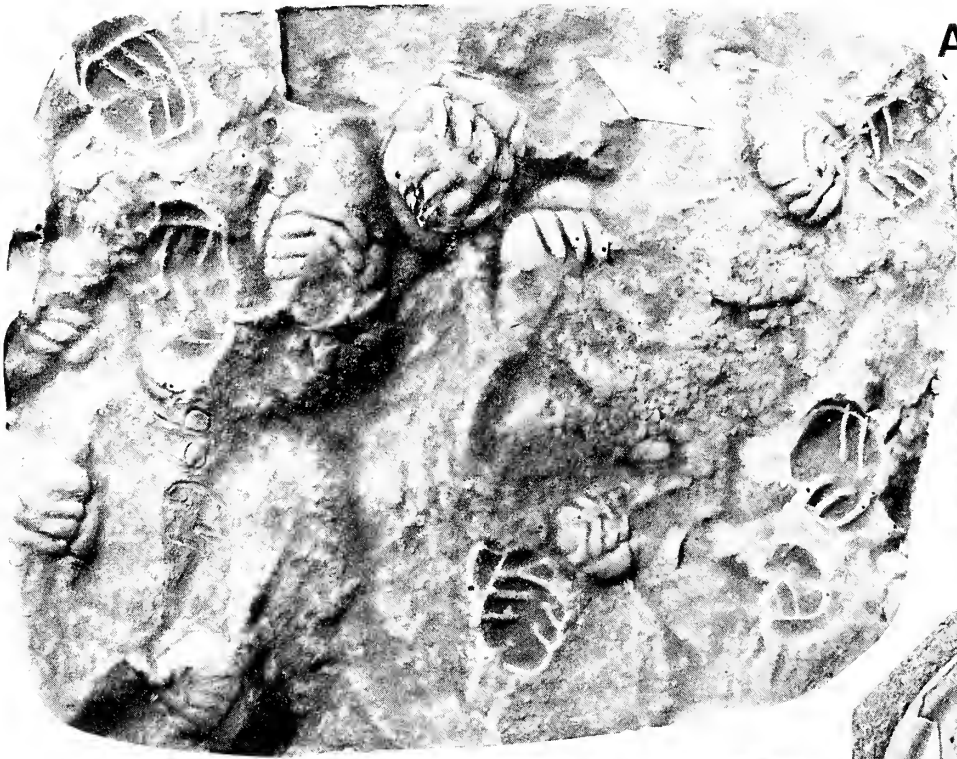
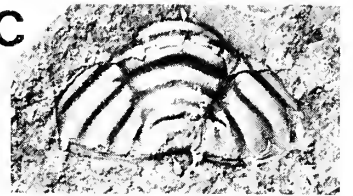


Figure 13. Probable phylogeny of eastern North American species of *Triarthrus* (*Triarthrus*) and *T. (Danarcus)*.



A

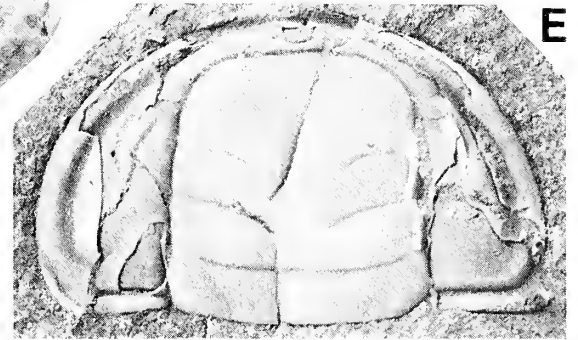
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D

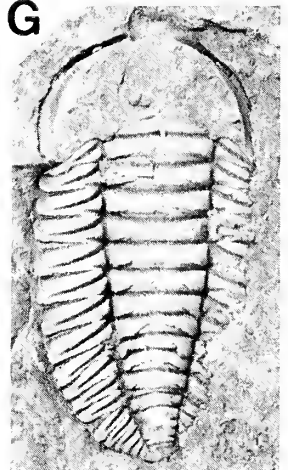


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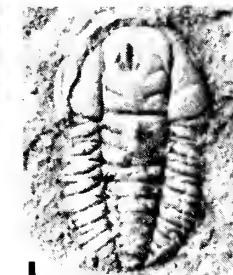
B



H



I



J



K



Plate 1. *Triarthrus* (*Triarthrus*) species. *A, B, Triarthrus* (*Triarthrus*) *beckii* Green, 1832. *A*, Plaster replica of type slab distributed by Jacob Green, USNM 4966, x1.8, Snake Hill Formation, Cohoes Falls, New York. *B*, Two cranidia, NYSM 9892, x3.5, lower Utica Shale, Rouses Point, New York. *C-K, Triarthrus* (*Triarthrus*) *eatoni* (Hall, 1838). *C*, Pygidium, ROM 45072, x5.5, lower Whitby Formation, Darlington, Ontario (Section TO-5, 50 cm above base of formation). *D*, Cranidium, NYSM 9895, x5.0, Whetstone Gulf Shale, Mill Creek, New York. *E*, Cephalon, ROM 43105, x5.0, lower Whitby Formation, Ottawa, Ontario (drill hole OW-2, 9 m above base of formation). *F*, Small exoskeleton (latex impression), ROM 45073, x7.0, lower Whitby Formation, Billings Bridge, Ottawa, Ontario. *G*, Small exoskeleton without cranidium, GSC 1939c, x4.0 (paratype of *T. glaber* Billings), Pointe-Bleue Shales, Lac St. Jean, Quebec. *H*, Yoked cheeks, ROM 45074, x3.0, lower Whitby Formation, Darlington, Ontario (section TO-5, 70 cm above base of formation). *I*, Degree 6 meraspid, ROM 45075, x9.0, lower Whitby Formation, Billings Bridge, Ottawa, Ontario. *J*, Cranidium, neotype, NYSM 9894, x3.5, Utica Shale, Oxtungo Creek, near Fort Plain, New York. *K*, Cranidium, YPM 26271, x5.0 (paratype of *T. becki macastyensis* Twenhofel), Macasty Formation, Port Menier, Anticosti Island, Quebec.

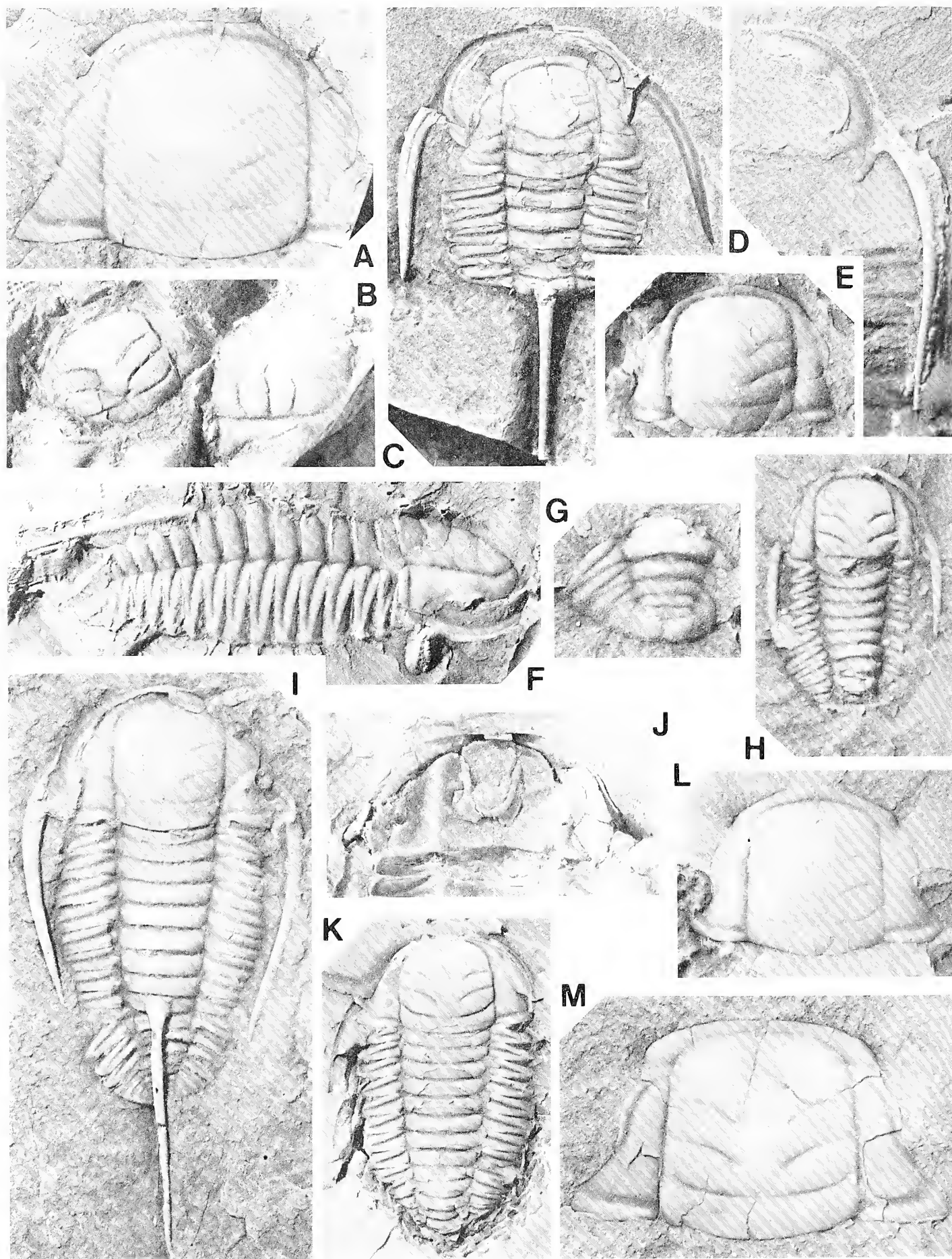


Plate 2. *Triarthrus* (*Triarthrus*) species. *A-M*, *Triarthrus* (*Triarthrus*) *rougensis* Parks, 1921. *A*, Cranidium, ROM 45079, x4.0, upper Whitby Formation, Toronto, Ontario (drill hole TO-1, 15.58 m above base of formation). *B*, Two cranidia, GSC 6780b, x4.5 (syntypes of *T. hugusensis* Foerste), Lorraine Formation, Yamaska River, Quebec. *C*, Exoskeleton with displaced yoked cheeks, GSC 70985, x3.0, lower Whitby Formation, Ottawa, Ontario. *D*, Free cheek, ROM 45080, x4.0, upper Whitby Formation, Collingwood, Ontario (drill hole CW-9, 8.66 m above base of formation). *E*, Cranidium, ROM 45081, x4.5, upper Whitby Formation, Collingwood, Ontario (drill hole CW-6, 21.08 m above base of formation). *F*, Exoskeleton (latex impression), ROM 45082, x2.5, upper Whitby Formation, Collingwood, Ontario (drill hole CW-2, 27.89 m above base of formation). *G*, Pygidium, ROM 45083, x5.5, upper Whitby Formation, Collingwood, Ontario (drill hole CW-7, 23.31 m above base of formation). *H*, Exoskeleton (latex impression), ROM 431 14, x7.5, upper Whitby Formation, Manitoulin Island, Ontario (drill hole MT-2, 14.00 m above base of formation). *I*, Exoskeleton (latex impression), holotype, ROM 25710, x4.5, upper Whitby Formation, Rouge River, 2 km north of Kingston Road Bridge, Toronto, Ontario. *J*, Cephalon, note hypostome attached to doublure, ROM 45084, x3.0, upper Whitby Formation, Section CW-11, Collingwood, Ontario. *K*, Exoskeleton, ROM 18802, x2.0 (holotype of *T. spinosus narrawayi* Parks), lower Whitby Formation, Billings Bridge, Ottawa, Ontario. *L*, Cranidium, ROM 43112, x4.5, upper Whitby Formation, Bolton, Ontario (drill hole BO-1, 28.61 m above base of formation). *M*, Cranidium, ROM 43115, x3.5, upper Whitby Formation, Bolton, Ontario (drill hole BO-1, 11.49 m above base of formation).

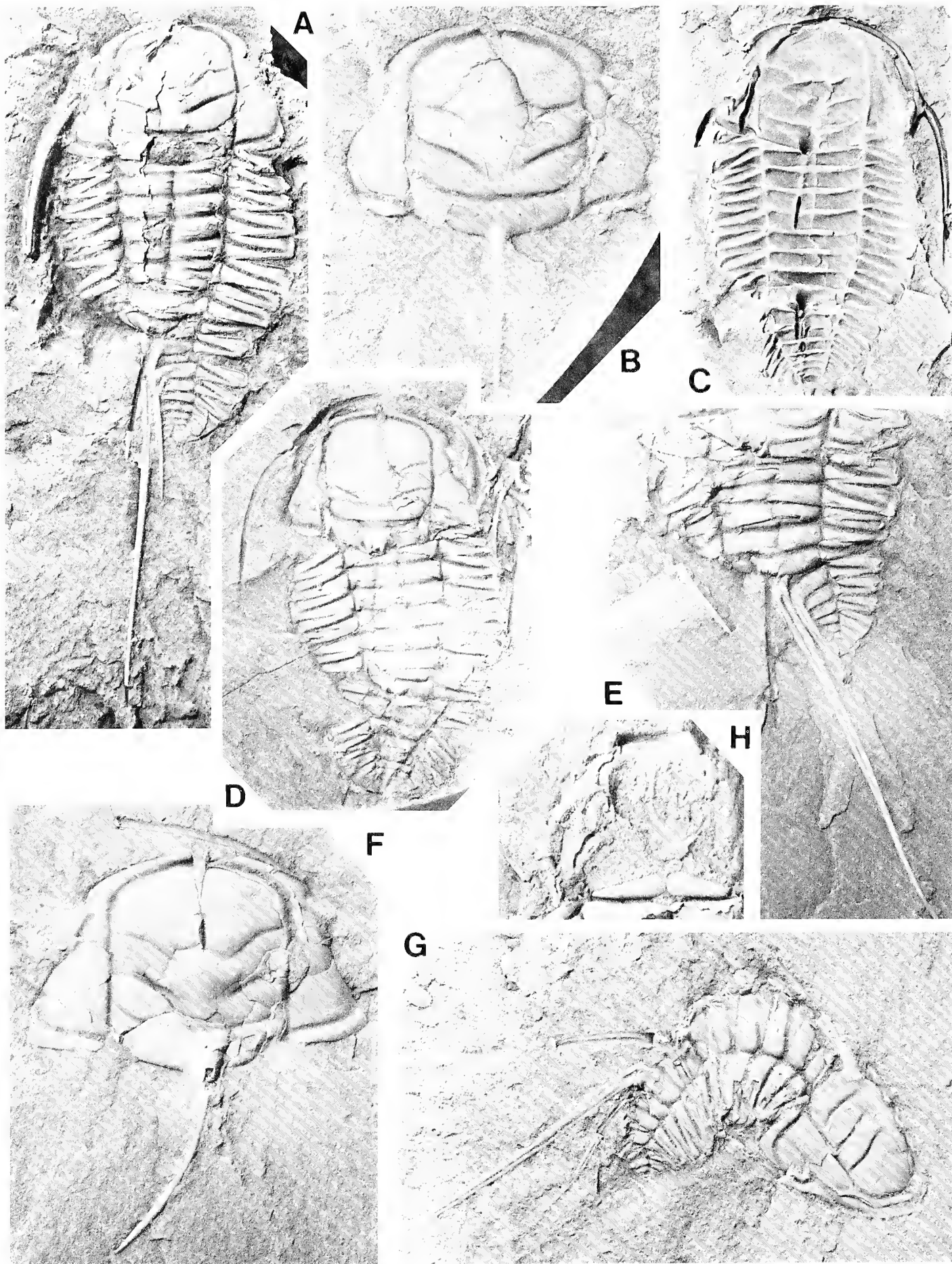


Plate 3. *Triarthrus (Triarthrus)* species. *A-G, Triarthrus (Triarthrus) spinosus* Billings, 1857. *A*, Exoskeleton, GSC 1936, x3.0, lower Whitby Formation, Cummings Bridge, Ottawa, Ontario. *B*, Cranidium, ROM 45085, x4.5, lower Whitby Formation, Ottawa, Ontario (drill hole OW-2, 12.65 m above base of formation). *C*, Exoskeleton, probably the holotype, GSC 1938a, x4.5, Whitby Formation, Rideau River, Lot 17. Gloucester Township, Ottawa, Ontario. *D*, Exoskeleton, ROM 18800a, x3.0, lower Whitby Formation, Ottawa, Ontario. *E*, Thorax and pygidium, ROM 18800b, x3.5, lower Whitby Formation, Ottawa, Ontario. *F*, Cranidium, GSC 13616, x4.0, Whitby Formation, Gloucester Township, Ottawa, Ontario. *G*, Exoskeleton, laterally compressed, USNM 96235, x2.5, Whitby Formation, Gloucester Township, Ottawa, Ontario. *H, Triarthrus (Triarthrus) eatoni* (Hall, 1838), yoked cheeks and hypostome, ROM 45086, x5.5, Macasty Formation, Port Menier, Anticosti Island, Quebec.

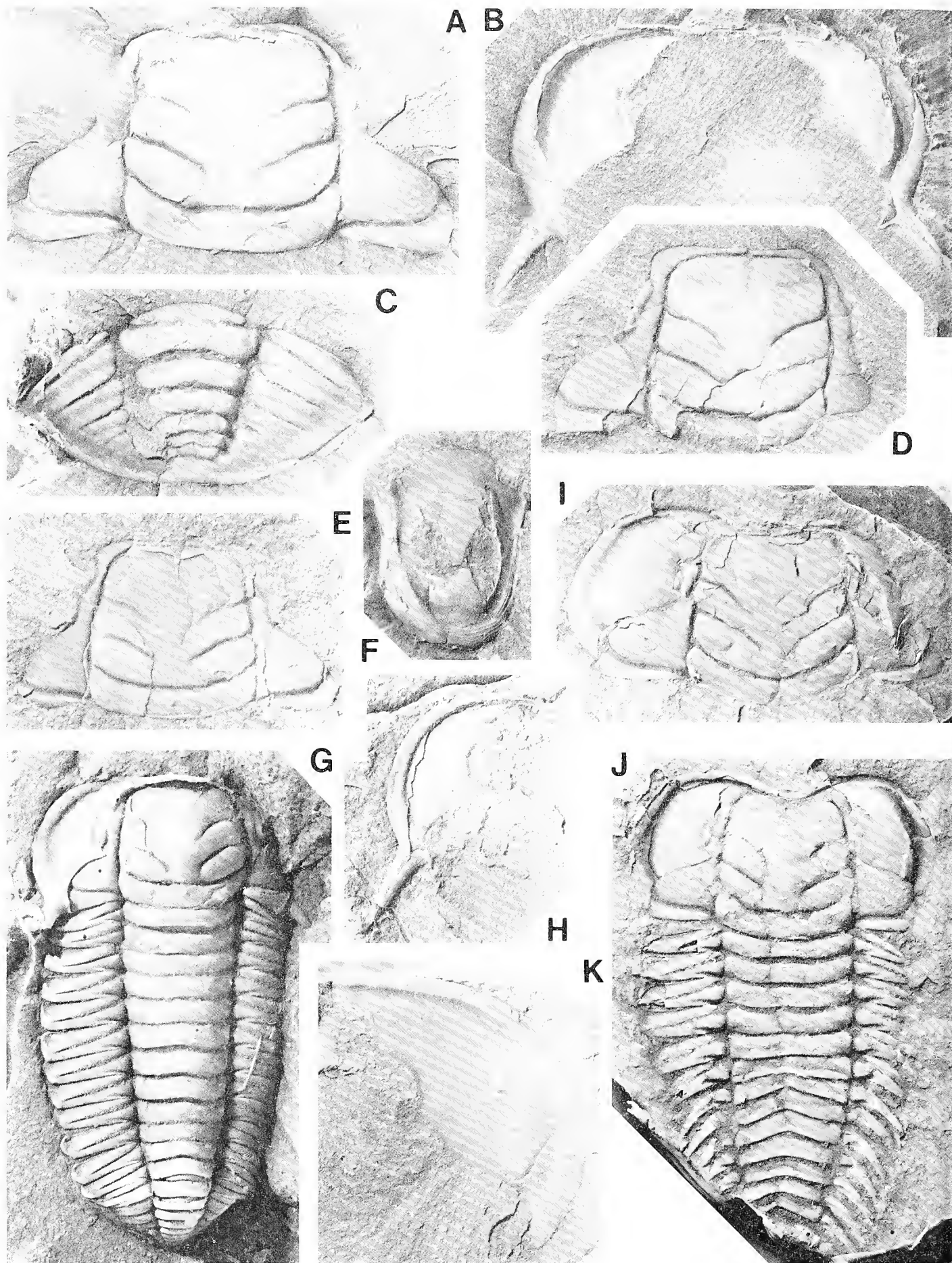


Plate 4. *Triarthrus (Danarcus)* species. *A-H, Triarthrus (Danarcus) canadensis* Smith, 1861. *A*, Cranidium, ROM 45076, x3.5, upper Whitby Formation, Toronto, Ontario (drill hole TO-4, 29.05 m above base of formation). *B*, Yoked cheeks, neotype, ROM 43106, x3.5, upper Whitby Formation, Toronto, Ontario (drill hole TO-4, 22.65 m above base of formation). *C*, Pygidium, ROM 43104, x3.5, upper Whitby Formation, Toronto, Ontario (drill hole TO-4, 22.45 m above base of formation). *D*, Cranidium, ROM 43110, x3.0, lower Whitby Formation, Toronto, Ontario (drill hole TO-3, 8.91 m above base of formation). *E*, Cranidium, ROM 43107, x4.5, upper Whitby Formation, Toronto, Ontario (drill hole TO-3, 10.23 m above base of formation). *F*, Hypostome, ROM 45077, x5.0, upper Whitby Formation, Toronto, Ontario (drill hole TO-1, 22.49 m above base of formation). *G*, Exoskeleton (latex impression), ROM 25188, x1.8, upper Whitby Formation, Rouge River, 2 km north of Kingston Road Bridge, Toronto, Ontario. *H*, Free cheek, ROM 25188, x5.0, Whitby Formation, Craigleith, Ontario. *I-K, Triarthrus (Danarcus) glaber* Billings, 1859. *I*, Cephalon, GSC 1939g, x1.8, Pointe-Bleue Shales, Lac St. Jean, Quebec. *J*, Exoskeleton (latex impression), lectotype, GSC 1939f, x2.3, Pointe-Bleue Shales, Lac St. Jean, Quebec. *K*, Free cheek, ROM 45078, x3.5, upper Whitby Formation, Toronto, Ontario (drill hole TO-3, 10.10 m above base of formation).

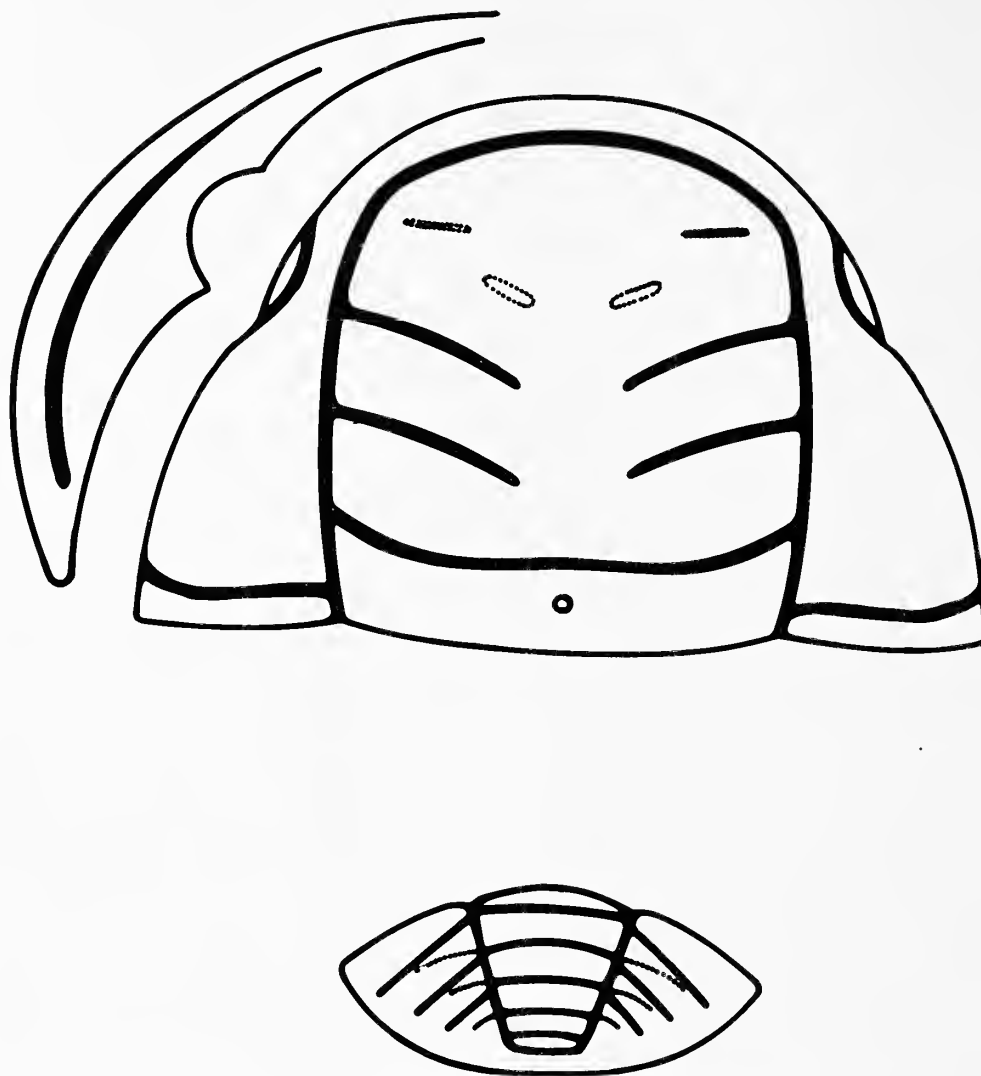


Figure 14. Reconstruction of cranidium, free cheek, and pygidium of *Triarthrus* (*Triarthrus*) *beckii* Green, 1832.

figs. 1-13 [= *T. (T.) beckii*]; ROSS, 1979, p. 2, Pl. 1, figs. 1-13 [= *T. (T.) beckii*].

Diagnosis.—A species of *Triarthrus* (*Triarthrus*) with long palpebral lobes located opposite 2S furrows, a parallel-sided glabella, and rounded genal corners.

Neotype.—No specimen matching that illustrated by Hall (1838, fig. 2) could be located in the James Hall collections kept at the New York State Museum, the American Museum of Natural History, the Field Museum of Natural History, the U.S. National Museum of Natural History, the University of California at Berkeley, Beloit College, the Peabody Museum of Natural History, or the Milwaukee Public Museum.

The original specimens of *Triarthrus eatoni* came from "the greywacke slate in Turin, Utica, Fort Plain," or Frankfort Formation. The neotype selected here is the large cranidium from the Utica Shale at Oxtungo Creek near Fort Plain, New York State, that was illustrated by Ruedemann (1926, Pl. 21, fig. 8). This specimen (NYSM 9894, Plate 1, figure J) conforms closely to the original species concept.

Occurrences.—Frankfort Formation and Utica Shale (Edenian and lower Maysvillian) of New York State (Ruedemann, 1926). Lower and upper members of Whitby Formation (Maysvillian) of southern Ontario

(herein). Pointe-Bleue Shales (Maysvillian) of Lac St. Jean, Quebec (Desbiens and Lespérance, 1989). Upper Macasty Formation (Maysvillian) of Anticosti Island (Twenhofel, 1927; Ludvigsen and Tuffnell, 1983).

Remarks.—As has now been finally determined, the celebrated pyritized specimens of *Triarthrus* with preserved appendages from the Frankfort Formation of New York belong to *T. (T.) eatoni* and not to *T. (T.) beckii* (Ludvigsen and Tuffnell, 1983; Whittington and Almond, 1987).

TRIARTHURUS (TRIARTHURUS) ROUGENSIS Parks, 1921

Plate 2, figures A-M; Figure 16

Triarthrus spinosus rougensis PARKS, 1921, p. 51, Pl. 1, figs. 7, 8, 11; PARKS, 1928, p. 89, Fig. 25.

Triarthrus huguesensis FOERSTE, 1924, p. 241, Pl. 43, fig. 21.

Triarthrus spinosus narrawayi PARKS, 1928, p. 89.

Triarthrus rougensis PARKS. LUDVIGSEN AND TUFFNELL, 1983, Pl. 1, figs. 6, 7, Pl. 2, fig. 3; TUFFNELL AND LUDVIGSEN, 1984, p. 14, Pl. 3, figs. 3-12; DESBIENS AND LESPÉRANCE, 1989, Fig. 3G.

Diagnosis.—A species of *Triarthrus* (*Triarthrus*) with long sinuous

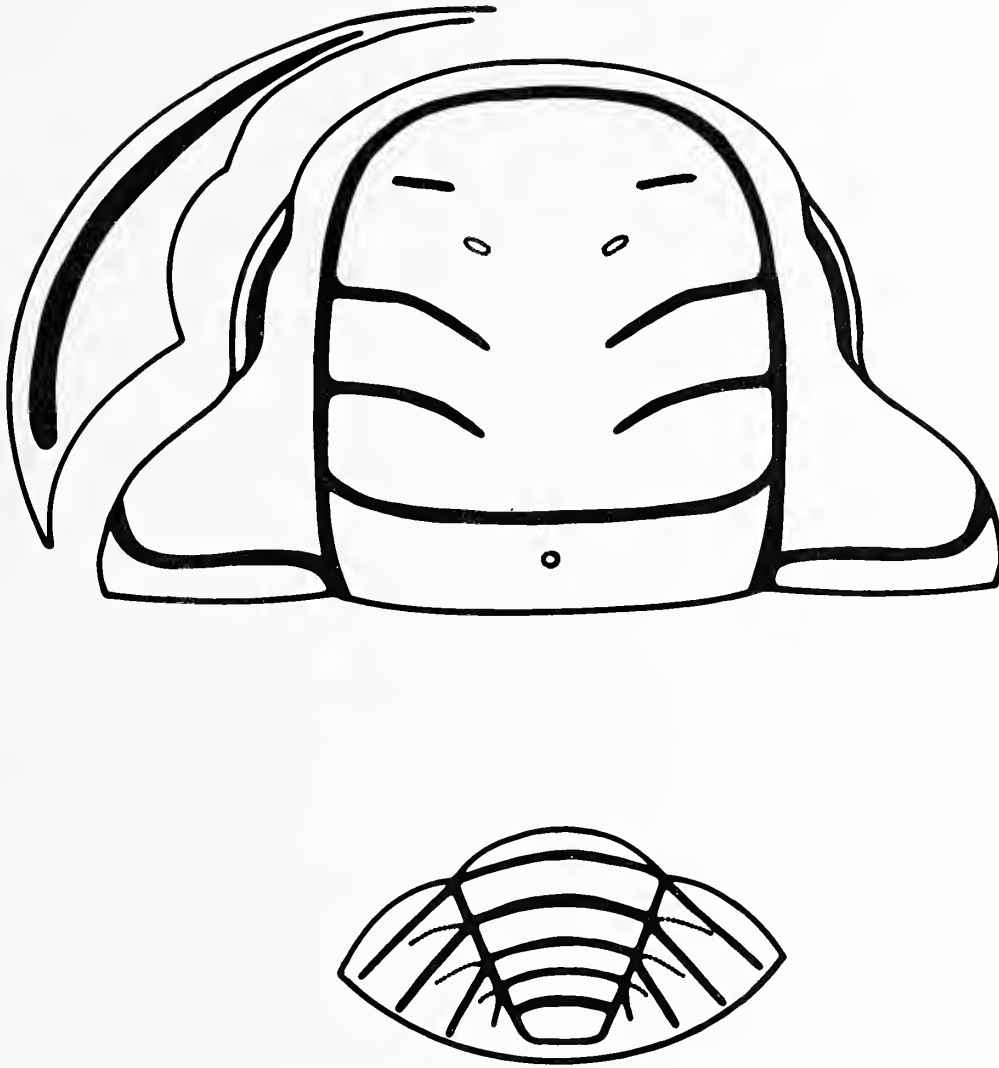


Figure 15. Reconstruction of cranidium, free cheek, and pygidium of *Triarthrus* (*Triarthrus*) *eatoni* (Hall, 1838).

palpebral lobes located opposite 2P lobes, a median spine of the 9th thoracic segment, and long slender genal spines.

Holotype.—An external mold of an exoskeleton from the upper Whitby Formation on the Rouge River, Toronto (ROM 25710, Plate 2, figure 1).

Occurrences.—Lower and upper members of the Whitby Formation (Maysvillian and early Richmondian) of southern Ontario (Parks, 1928; herein). Pointe-Bleue Shales (Maysvillian) of Lac St. Jean, Quebec (Desbiens and Lespérance, 1989). Nicolet River Formation (Maysvillian) of St. Lawrence Valley (Foerste, 1924; herein).

Remarks.—Even in the absence of the characteristic free cheeks with long slender genal spines, specimens of *Triarthrus* (*T.*) *rougensis* are readily distinguished on the basis of their long sinuous palpebral lobes and the relatively wide fixed cheek in front of the low palpebral ridge.

TRIARTHURUS (TRIARTHURUS) SPINOSUS Billings, 1857
Plate 3, figures A-G; Figure 17

Triarthrus spinosus BILLINGS, 1857, p. 340; LOGAN, 1863, Fig. 199; AMI, 1883, p. 88, unnumbered Pl. and fig.; PARKS, 1921, p. 50, unnumbered Pl., fig. 9; RUEDEMANN, 1926, p. 121, Pl. 21, figs. 13-16; KAY, 1937, Pl. 10, unnumbered fig.; WILSON, 1956, Pl. 5, figs. 3, 4; LIBERTY, 1964, Pl. 5, fig. 5; BOLTON, 1970, Pl. 6, fig. 7; NORFORD ET AL., 1970, Pl. 4, fig. 23; LUDVIGSEN, 1978, Pl. 6, fig. 55; LUDVIGSEN, 1979a, Fig. 39C; LUDVIGSEN AND TUFFNELL, 1983, Pl. 1, figs. 2, 3, Pl. 2, figs. 4, 5; TUFFNELL AND LUDVIGSEN, 1984, p. 16, Pl. 4, figs. 1-6; DESBIENS AND LESPÉRANCE, 1989, Fig. 3E, F.

Diagnosis.—A species of *Triarthrus* (*Triarthrus*) with short palpebral lobes located opposite 2S furrow, an occipital spine, long median spines on the 8th, 9th, and 10th thoracic segment, and long slender genal spines.

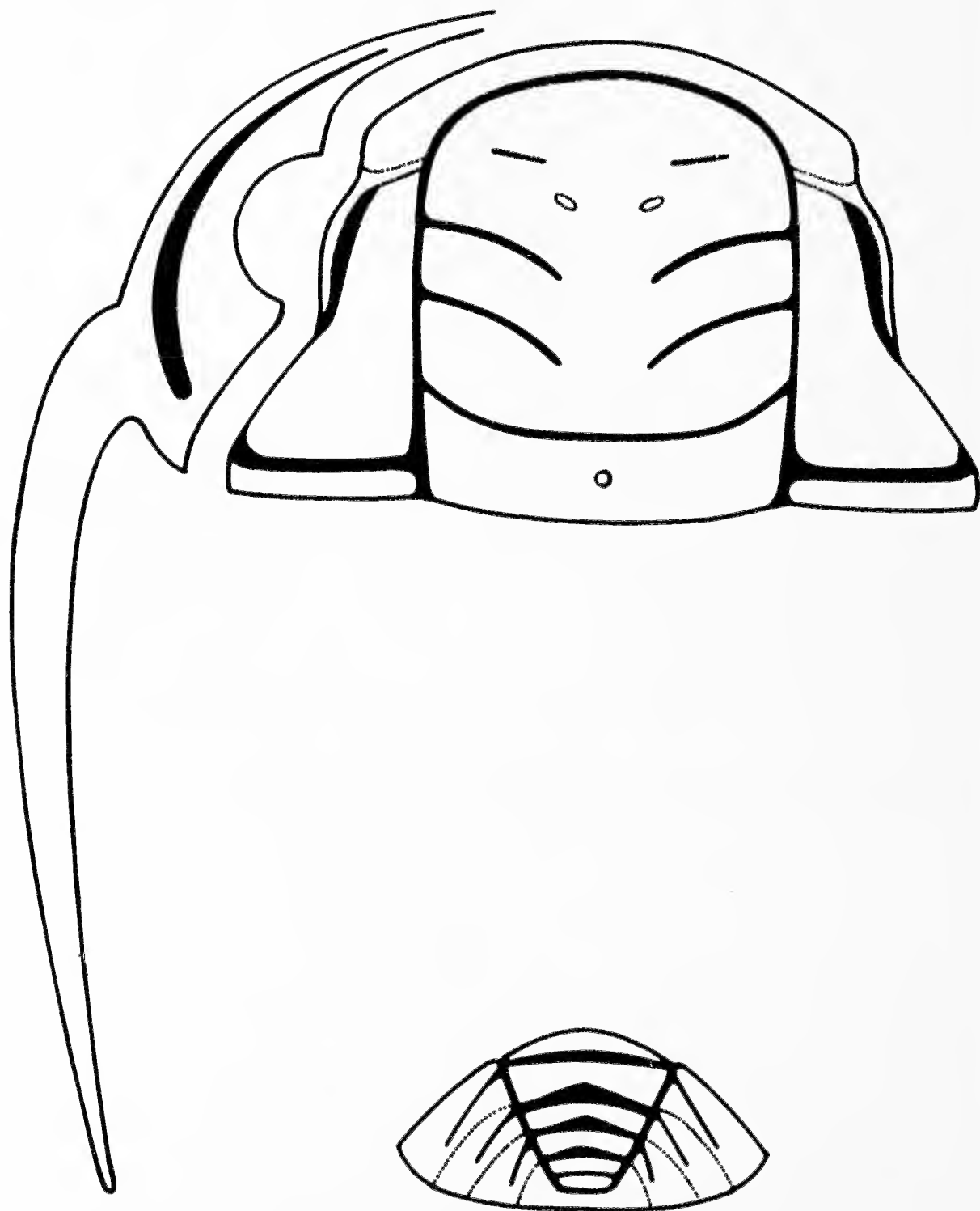


Figure 16. Reconstruction of cranidium, free cheek, and pygidium of *Triarthrus (Triarthrus) rougensis* Parks, 1921.



Figure 17. Reconstruction of cranidium, free cheek, and pygidium of *Triarthrus (Triarthrus) spinosus* Billings, 1857.

Holotype.—The holotype, a complete specimen from the Whitby Formation in Gloucester Township, Carleton County, Ontario (Logan, 1863, fig. 199), has not been identified with certainty in the collections of the Geological Survey of Canada. However, an external mold of a complete specimen that was collected by Elkanah Billings from the Utica "Slate," Lot 17 in Gloucester Township, agrees well with Logan's illustrations, and that specimen is probably the holotype of *Triarthrus (T.) spinosus* (GSC 1938a; Plate 3, Figure C). The median spine on the 8th thoracic segment of this specimen partly overlaps the spines on the 9th

and 10th segments. This is possibly the explanation of why Billings (1857) described *T. spinosus* as having only a single median thoracic spine.

Occurrences.—Lower Whitby Formation (Maysvillian) of the Ottawa area (Ami, 1883; herein). Pointe-Bleue Shales (Maysvillian) of Lac St. Jean, Quebec (Desbiens and Lespérance, 1989). Utica Formation (Maysvillian) of New York State (Ruedemann, 1926).

Remarks.—Both Ami (1883) and Ruedemann (1926) speculated that each thoracic segment behind the 8th carries a median spine. The

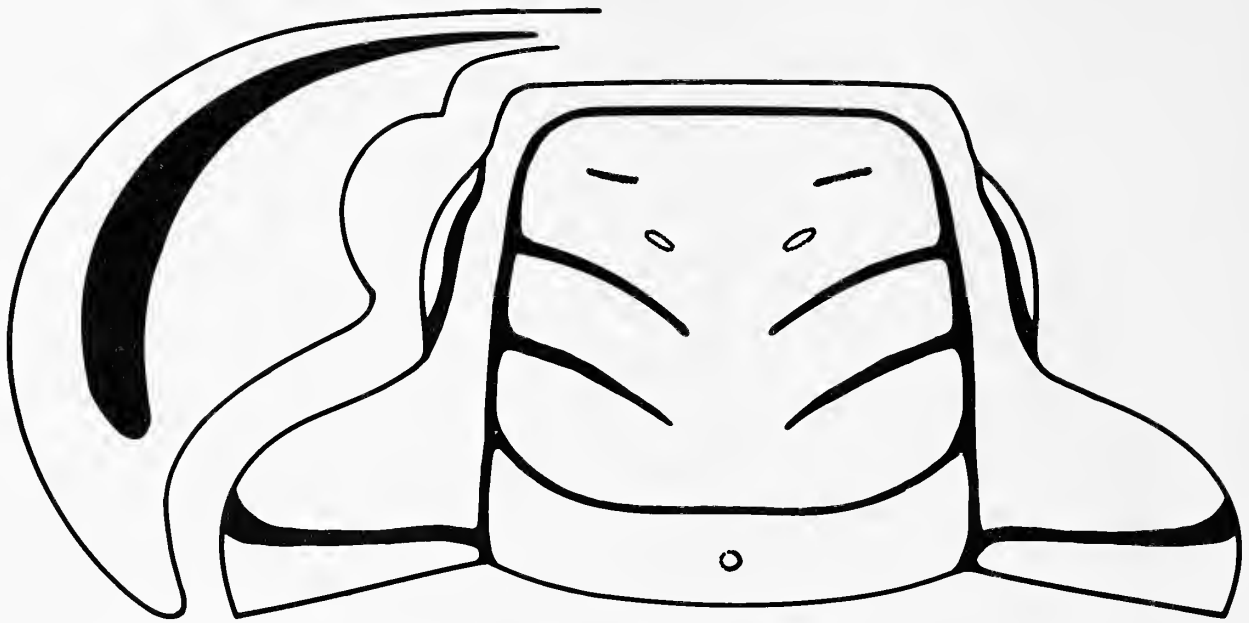


Figure 18. Reconstruction of cranidium and free cheek of *Triarthrus (Danarcus) glaber* Billings, 1859.

complete specimens illustrated herein (Plate 3, figures A, E, H) clearly show that *Triarthrus (T.) spinosus* possesses only three thoracic spines; the 11th and 12th segments lack spines.

Subgenus TRIARTHURUS (DANARCUS) n. subgen.

Type species.—*Triarthrus glaber* Billings, 1859, from the Pointe-Bleue Shales at Lac St. Jean, Quebec (Maysvillian).

Diagnosis.—A subgenus of *Triarthrus* with transversely oval cephalon that is strongly arched, a forwardly tapering glabella with a transverse front margin, wide free cheeks, and a large pygidium with a convex border.

Species assigned.—Two species from eastern North America [*Triarthrus (Danarcus) glaber* Billings, 1859 and *T. (D.) canadensis* Smith, 1861].

Name.—For James Dwight Dana, whose contribution to *Triarthrus* taxonomy has been almost entirely forgotten, plus *arcus* (L.)—a bow, in reference to the high anterior cephalic arch. Gender—masculine. Dana was the *de facto* author of Hall (1838)—Hall's first paper in a scientific journal and the first to deal with fossils (Ludvigsen, 1991).

TRIARTHURUS (DANARCUS) GLABER Billings 1859

Plate 4, figures I-K, Figure 18

Triarthrus glaber BILLINGS, 1859, p. 382; LOGAN, 1863, Fig. 198; LUDVIGSEN AND TUFFNELL, 1983, Pl. 3, figs. 5-7; DESBIENS AND LESPÉRANCE, 1989, Fig. 3C, D.

Triarthrus huguesensis Foerste. BOLTON, 1970, p. 38, Pl. 6, figs. 1-6, 24.

?*Triarthrus* spp. WORKUM ET AL., 1976, Pl. 3, figs. 3, 8.

not *Triarthrus glaber* Billings. PARKS, 1928, p. 89, fig. 26 [= *T. (D.) canadensis*].

Diagnosis.—A species of *Triarthrus (Danarcus)* lacking genal spines.

Lectotype.—A nearly complete external mold of an exoskeleton

from the Pointe-Bleue Shales (Desbiens and Lespérance, 1989) at Lac St. Jean (GSC 1939, Plate 4, figure J) was selected as lectotype by Ludvigsen and Tuffnell (1983).

Occurrences.—Pointe-Bleue Shales (Maysvillian) of Lac St. Jean, Quebec (Desbiens and Lespérance, 1989; herein). Lower Vaureal Formation (Maysvillian) of Anticosti Island (Bolton, 1970). A single free cheek occurs in the upper member of the Whitby Formation (Maysvillian) in southern Ontario (herein). Possibly occurs in unnamed shales (Maysvillian or Richmondian) on Akpatok Island, Quebec (Workum et al., 1976).

Remarks.—*Triarthrus (Danarcus) glaber* is almost entirely restricted to Maysvillian shales in Quebec. Parks (1928) claimed that this species is abundant at the Rouge River exposures of the upper Whitby in the Toronto area, but these cranidia probably belong to *T. (D.) canadensis*—a species that is very common in this area and one that cannot be distinguished from *T. (D.) glaber* on cranidial characteristics alone. *Triarthrus (D.) glaber* does occur in Ontario, but it is extremely rare—only a single specimen is known.

TRIARTHURUS (DANARCUS) CANADENSIS Smith, 1861

Plate 4, figures A-H; Figure 19

Triarthrus canadensis SMITH, 1861, p. 175, Fig. 1; PARKS, 1921, p. 47, Pl. 1, figs. 1-4, 10; PARKS, 1928, p. 90, Fig. 27; LUDVIGSEN AND TUFFNELL, 1983, Pl. 1, fig. 4, Pl. 2, figs. 1, 2; TUFFNELL AND LUDVIGSEN, 1984, p. 15, Pl. 2, figs. 5-9, Pl. 3, figs. 1, 2; JOHNSON AND RONG, 1989, Fig. 3 S-W, a-f.

Triarthrus glaber Billings. PARKS, 1928, p. 89, fig. 26.

Triarthrus cf. *glaber/canadensis* of PARKS, 1928, p. 90, Fig. 28.

Diagnosis.—A species of *Triarthrus (Danarcus)* with short, stout genal spines.

Neotype.—Searches of the Royal Ontario Museum and the Geological Survey of Canada collections failed to locate Smith's holotype of *Triarthrus canadensis*. This is a specimen with yoked cheeks

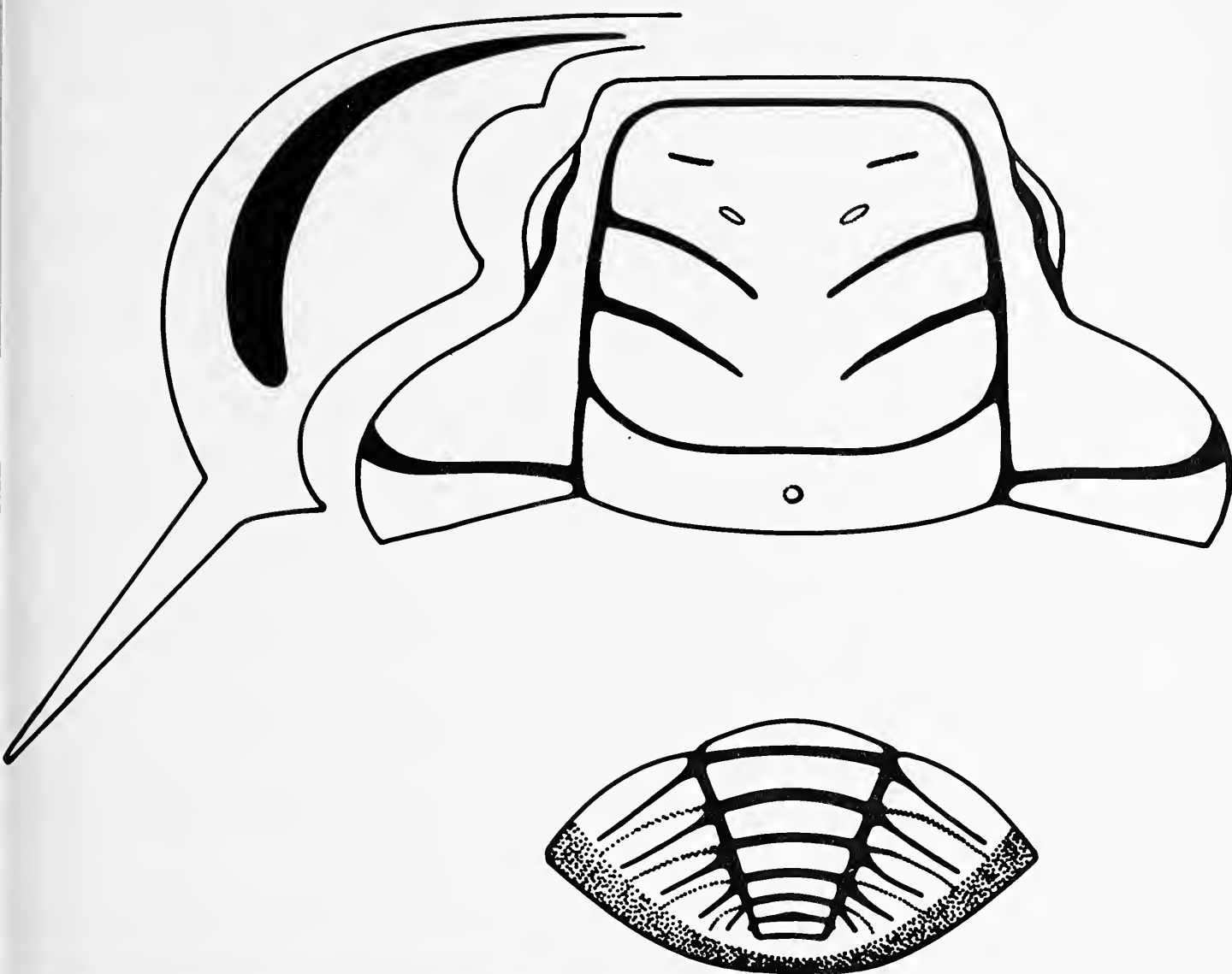


Figure 19. Reconstruction of cranidium, free cheek, and pygidium of *Triarthrus* (*Danarcus*) *canadensis* Smith, 1861.

from the Whitby Formation at Whitby, Ontario. As a neotype, a specimen with nearly identical yoked cheeks is selected herein (ROM 43106, Plate 4, figure B) from the upper member of the Whitby Formation at drill hole TO-4 in downtown Toronto.

Occurrences.—Lower and upper members of the Whitby Formation (Maysvillian) of southern Ontario (Parks, 1928; Johnson and Rong, 1989; herein).

Remarks.—The only consistent difference between *Triarthrus* (*Danarcus*) *canadensis* and *T. (D.) glaber* is the presence of stout genal spines. Parks (1928) postulated a continuum between these two species that is recorded by a gradation of spine lengths. However, only a single specimen (ROM 205U) with an intermediate spine length was identified by Parks. Examination of this poorly preserved specimen reveals that the genal spines are not short, but merely broken.

Triarthrus (D.) canadensis occurs only in the Maysvillian of Ontario, whereas its sister species *T. (D.) glaber* is almost entirely

restricted to the Maysvillian of Quebec. These “two solitudes” provide an excellent example of allopatric species.

Acknowledgments

This project on biostratigraphy and taxonomy of *Triarthrus* from the Whitby Formation was made possible by a research contract with the Ontario Geological Survey. We thank P.G. Telford for facilitating this work and for permission to sample the OGS core for trilobites and graptolites. Additional financial support came from NSERC Operating Grant A3825 to R. Ludvigsen at the University of Toronto. J. Smith assisted in the field. J. Riva of Université Laval identified all graptolites from the Whitby core. Careful reviews by B.D.E. Chatterton, J. Cisne, and S.R. Westrop improved the paper considerably. The University of Victoria supplied \$1,200 toward publication of this report.

We dedicate this paper to the memory of our friend Brian

O'Donovan, recently deceased photographer at the Department of Geology, University of Toronto, whose skill and commitment to his craft are recorded in all publications on trilobites that came out of the University of Toronto during the 1970s and 1980s.

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Upper Precambrian–Cambrian faunal sequence, Sonora, Mexico, and Lower Cambrian fossils from New Jersey, United States

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Abstract

One hundred and sixty-two different types of marine organisms have been reported from the Vendian–Cambrian sedimentary sequence of the Caborca region, Sonora, Mexico, whereas only seven different Lower Cambrian species have been recognized in the Franklin, New Jersey, area. The vast inequality in the diversity of fossils recognized from the two areas is testimony to the vagaries of preservation. A compendium follows of all the Vendian and Cambrian organisms known from both localities. The lower Leithsville Formation of New Jersey is correlated herein with the Buelna Formation of Sonora on the basis of similarities between archaeocyathans and the fact that both formations occur downsection from upper Lower Cambrian disconformities.

The Mexican sequence

The Caborca region of northwestern Sonora, Mexico, is in the Altar Desert, an area characterized by northwest-trending hills and mountain ranges; the region is best known to geologists for its rich gold deposits (Emmons, 1937) and the major strike-slip fault known as the “Mojave Sonora megashear” (De Jong et al., 1988). The older sedimentary rocks in the region are allochthonous; thrust sheets bearing the fossiliferous Vendian and Cambrian strata (Figure 1) have been dislocated to the west (De Jong et al., 1988). These strata have produced a rich biota of Upper Precambrian and Lower to Middle Cambrian marine fossils (Cooper et al., 1952, 1956; McMenamin et al., 1983; McMenamin, 1984, 1985, 1987a; Stewart et al., 1984; McMenamin and McMenamin, 1990; see Plate 1.1, 1.3, 1.5, 1.6). These fossils are preserved in shallow-water, mixed siliciclastic–carbonate sediments. The section is of particular interest because a volcanoclastic conglomerate and possible volcanic flows are present in the Cambrian Puerto Blanco Formation. The volcanic rocks are pervasively altered, possibly as a result of subaqueous eruption, although no pillow structures have been positively identified. Thin-sectioned samples of the volcanic rocks from the Cerro Rajón area (unit 1 of the Puerto Blanco Formation) include an ilmenite-rich metabasalt (sample 4 of 3/23/90b) and chlorite- and clinozoisite-rich porphyritic basalt (or possibly mafic andesite) with plagioclase phenocrysts up to 5 mm in diameter (sample 4 of 3/23/90; S. Dunn and M. Godchaux, personal commun., 1990).

The sequence seems to be remarkably continuous, considering the presumed shallow-water nature of the sediments; no major gaps or

unconformities are known in the sections above the basal nonconformity. Figure 1 shows a correlation of the strata between three of the cerros (hills or ranges) in the Caborca region: Cerros Calaveras, Cerros de la Proveedora, and the Cerro Rajón area. As Figure 1 indicates, individual formation thicknesses are fairly consistent throughout the region. The major exceptions to this pattern are the Middle Cambrian Tren Formation, which is truncated at the top of the section by a major unconformity, and the volcanoclastic rocks of unit 1 of the Puerto Blanco Formation, which are significantly thicker at Cerro Rajón than at the other two sections. The Cambrian part of the sequence is thought to have formed on the offshore edge of the middle carbonate belt (Fritz, 1975). The *Glossopleura* and *Albertella* Zones (Middle Cambrian), *Bonnina*–*Olenellus*, *Nevadella* and probably *Fallotaspis* Zones (Lower Cambrian) are present. Signor and Mount (1989) have argued that the *Fallotaspis* Zone is missing in the Caborca section, but the recent discovery of a second *Fallotaspis*-like trilobite cephalon from the region (unit 2 of the Puerto Blanco Formation, Cerro Clemente; sample 5 of 3/20/90) downsection from a new discovery of *Judomia orbis* (middle part of unit 3 of the Puerto Blanco Formation, Cerro Clemente; sample 2 of 3/20/90) supports, but does not prove, McMenamin's (1987a) contention that the *Fallotaspis* Zone is indeed present in the Caborca region. Trilobites and archaeocyathans occur down to the base of unit 2 of the Puerto Blanco Formation.

There is evidence, however, for several hiatuses in the Lower Cambrian part of the Caborca sequence. Grand Cycles are several hundred-meter-thick lithosomes that consist of a siliciclastic lower half and a carbonate upper half. Disconformities are commonly present between Grand Cycles. In Sonora, Grand Cycles A, B, and C can be recognized (Fritz, 1975; these are the same as Grand Cycles 1, 2, and 3 of Palmer, 1981). Grand Cycle A extends from the base of unit 2 of the Puerto Blanco Formation to approximately the middle part of unit 4 of this formation. A disconformity between units 1 and 2 of the Puerto Blanco Formation probably represents the loss of at least part of the *Fallotaspis* Zone, as well as some sub-*Fallotaspis* Zone strata. Grand Cycle B in Sonora is very thin and may be represented only by the upper half of unit 4 of the Puerto Blanco Formation. Gaps in the section are likely present both at the base of Grand Cycle B (just below the lowest occurrence of *Laudonia* in Puerto Blanco Formation unit 4) and at the boundary between the Puerto Blanco Formation and the Proveedora Quartzite, a boundary that marks the beginning of Grand Cycle C. The top of the Cerro Prieto Formation coincides with the top of Grand Cycle C. A stratigraphic hiatus is likely at this level in the section. Indeed, the

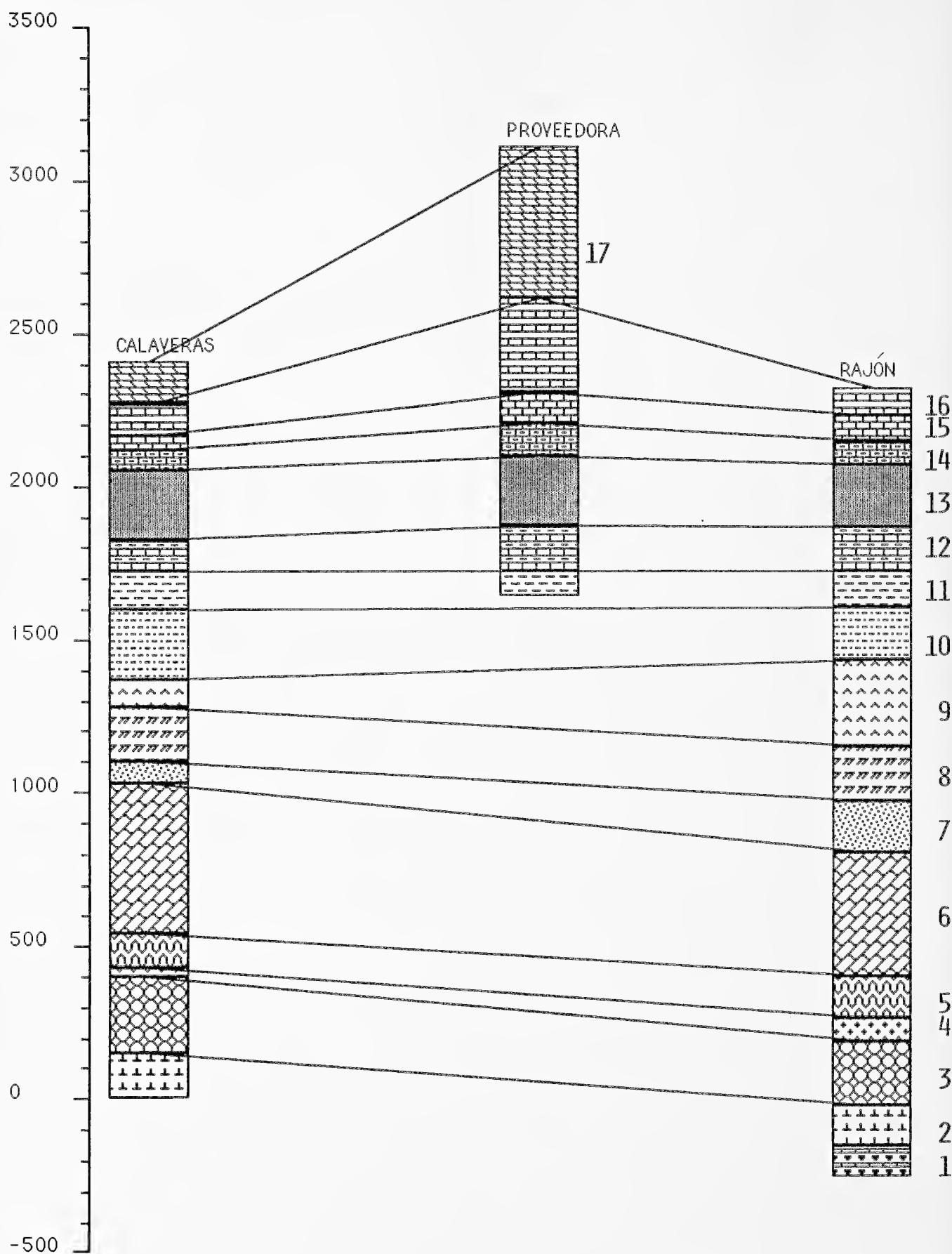


Figure 1. Correlation of three sections in the Caborca region. The formations and subdivisions thereof are represented as follows: (1) El Arpa Formation (primarily dolostones); (2) Caborca Formation (dolostones and siltstones); (3) Clemente Formation (mostly siltstone); (4) Pitiquito Quartzite (quartzite); (5) Gamuza Formation (dolostone); (6) Papalote Formation (dolostone); (7) Tecolote Quartzite (quartzite); (8) La Ciénega Formation (mixed dolostones and siliciclastics); (9) unit 1 of the Puerto Blanco Formation (volcaniclastics); (10) unit 2 of the Puerto Blanco Formation (siltstones); (11) unit 3 of the Puerto Blanco Formation (archaeocyathan limestones and siltstones); (12) unit 4 of the Puerto Blanco Formation (mixed limestones and siltstones); (13) Proveedora Quartzite (quartzite); (14) Buelna Formation (mixed limestones and siltstones); (15) Cerro Prieto Formation (limestone); (16) Arroyos Formation (mixed limestones and siltstones); (17) Tren Formation (dolostone). The Precambrian–Cambrian boundary is provisionally placed at the base of the La Ciénega Formation (8). Rock symbols used are diagrammatic and do not necessarily indicate any particular lithology. Thicknesses are in meters. Thickness data for the Cerros Calaveras from Eells (1972) and Longoria (1981); for the Cerros de la Proveedora from Cooper et al. (1952); for Cerro Rajón from Stewart et al. (1984). See Stewart et al. (1984, fig. 2) for a locality map of the sections plotted here.

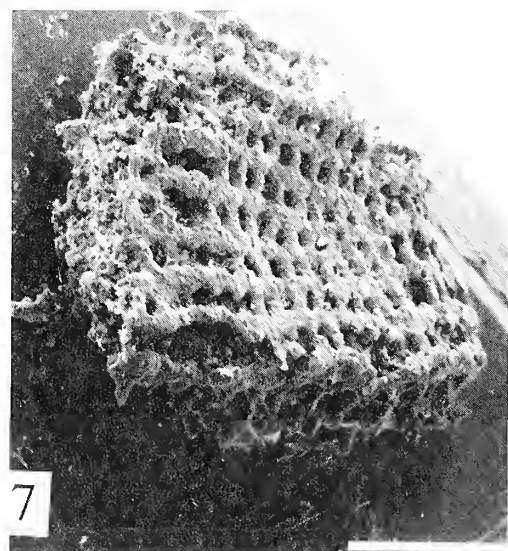
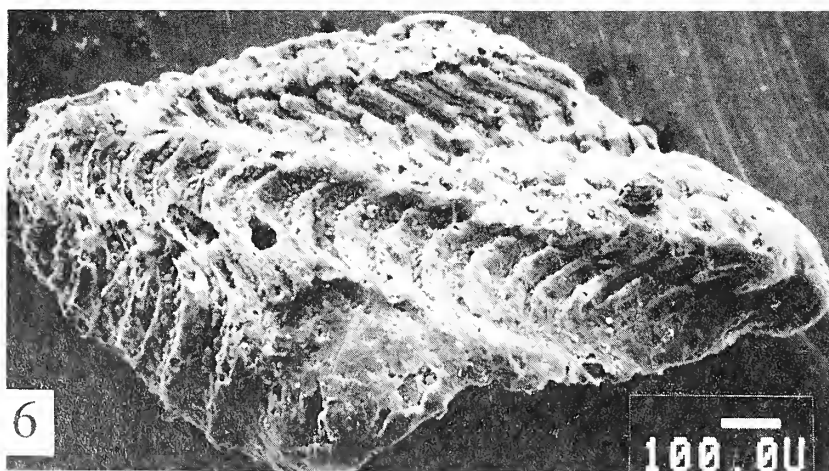
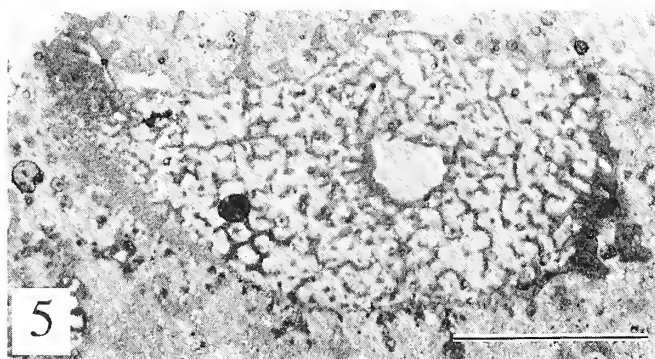
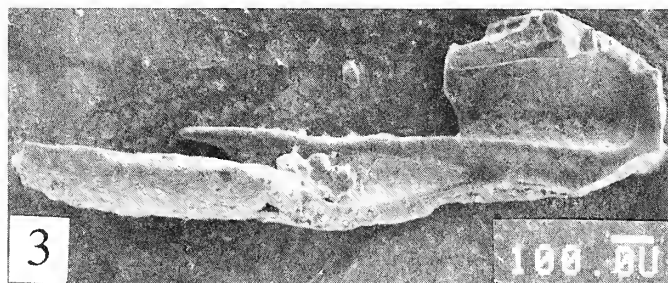
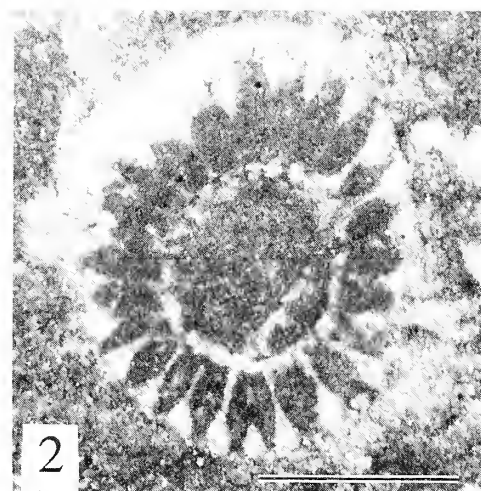
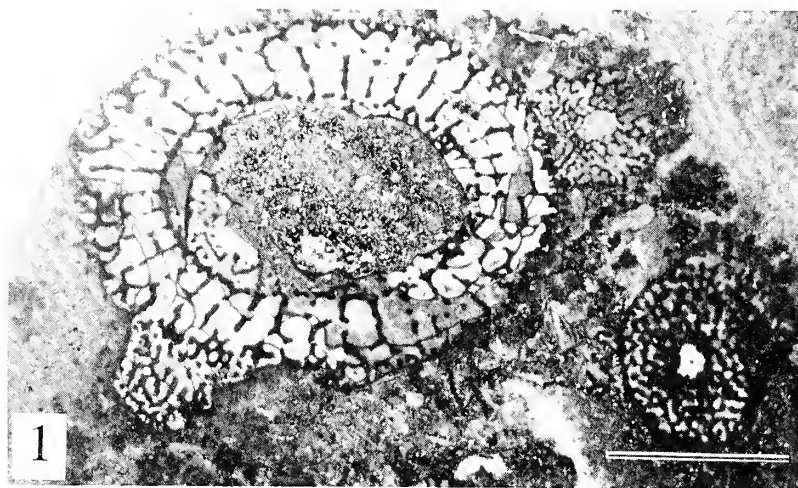


Plate 1. Cambrian fossils. 1, *Metaldetes* sp. with an attached *Dictyocyathus* sp. Two small *Dictyocyathus* are also present. Bar scale is 5 mm. Unit 3 of the Puerto Blanco Formation; Cerro Clemente, Sonora, Mexico; sample 1 of 12/15/82. Slide G by M. Carson, IGM 3661a. 2, Ajacicyathiid archeocyathan. The poor preservation has made this specimen hard to identify with any taxon lower than superfamily. Bar scale is 2.5 mm. Leithsville Formation; Franklin, New Jersey; sample 1 of 10/19/89. Slide 12 by E. Larrabee, NYSM 16133. 3, *Paiutitubulites* sp. Tube fragment showing inner septum. Bar scale is 0.1 mm. Unit 3 of the Puerto Blanco Formation; Cerro Clemente, Sonora, Mexico; sample 1 of 12/15/82; IGM 3614[39]. 4, Thin section from the Leithsville Formation. Transverse section of a hyolith? and cross-section through two trilobite segments. An unidentified archeocyath (possibly dictyocyathid) is also present. Bar scale is 3 mm. Leithsville Formation; Franklin, New Jersey; sample 1 of 10/19/89. Slide 12 by E. Larrabee, NYSM 16134. 5, *Protopharetra* sp. Bar scale is 2.5 mm. Unit 3 of Puerto Blanco Formation; Cerro Clemente, Sonora, Mexico; sample 1 of 12/15/82. Slide E by M. Carson, IGM 3661b. 6, *Lapworthella filigrana* Conway Morris and Fritz. Partially crushed specimen. Bar scale is 0.1 mm. Unit 3 of the Puerto Blanco Formation; Cerro Clemente, Sonora, Mexico; sample 2 of 12/15/82; IGM 3614[40]. 7, Silicified archaeocyathan. Oblique view of inner wall (this is the specimen mentioned in the "note added to proof" of McMenamin, 1987a, and discussed in Debrenne et al. (1989, p. 141). Bar scale is 1 mm. Base of unit 2 of the Puerto Blanco Formation; Cerro Rajón area, Sonora, Mexico; sample 4 of 12/17/82, IGM 3662.

Plagiura-Poliella Zone is partly, or perhaps entirely, absent in the Sonoran sections (Fritz, 1975; Stewart et al., 1984, fig. 8; but see Palmer, 1981, fig. 1A, which seems to indicate the presence of the *Plagiura-Poliella* Zone in Sonora.) Palmer (1981, p. 158) suggested that the next Grand Cycle top, Grand Cycle top 4, occurs in a limestone within the Arroyos Formation, and that the top of Grand Cycle 5 possibly occurs in a higher limestone within the Arroyos Formation. Gaps in the sequence might also be expected at these horizons within the Arroyos Formation.

The New Jersey fauna

Lower Cambrian fossils from Franklin, New Jersey, were first described by Palmer and Rozanov (1976), who recorded the presence of poorly preserved archaeocyathans in fluorite-rich fossiliferous packstones and wackestones of the Leithsville Formation. The fossils occur in a dark grey dolomitic limestone about 3 m above the top of a 4 m-thick quartzite in the lower part of the Leithsville Formation. This locality, used by Palmer and Rozanov (1976) as evidence for a major intra-Cambrian disconformity in New Jersey (the Hawke Bay Event), belongs to the *Bonnina-Olenellus* Zone.

All fossils from Franklin, New Jersey, have been identified in petrographic thin section (see Plate 1.2, 1.3, 1.7). Acetic acid etching of the carbonate produced no phosphatic shelly fossils, although some of the archaeocyathans did etch out in relief.

Correlation between the two sites

Interestingly, a fairly precise correlation can be made between the Mexican and New Jersey sites in spite of their geographic positions on opposite sides of North America. The archaeocyathan biota of the Leithsville Formation is of the upper middle *Bonnina-Olenellus* Zone according to Palmer and James (1979, p. 16, Fig. 2). This represents a slightly higher correlation of this biota than the lower *Bonnina-Olenellus* Zone correlation reported by Palmer and Rozanov (1976). The Leithsville Formation, therefore, correlates best with the Buelna Formation of Sonora and belongs to the upper middle *Bonnina-Olenellus* Zone. In fact, a representative of the Suborder Archaeocyathina reported from the upper Buelna Formation is similar to *Archaeocyathus* (= *Pycnocyathus*) and *Protopharetra* sp. of the Leithsville Formation, which also belong to the Suborder Archaeocyathina. Available material does not permit closer taxonomic comparison of these Mexican and New Jersey archaeocyathans, but they are clearly related forms.

Even more interestingly, the disconformity above the Leithsville fossils, which represents the Hawke Bay Event (Palmer and James, 1979), probably overlaps in age with the possible gap in the Sonoran sequence at the top of the Cerro Prieto Formation (the top of Grand Cycle C or 3), which is inferred here to represent at least partial loss of the basal Middle Cambrian *Plagiura-Poliella* Zone. It is therefore suggested that the Hawke Bay unconformity and the missing section at the top of Grand Cycle C represent consequences of the same event, and that both gaps record a eustatic event at the end of the Early Cambrian. This regressive event appears to have been worldwide, and has been implicated in the decimation of archaeocyathans as the Early Cambrian ended (Brasier, 1982).

Caborca faunal record

The compendium of fossils for both the Caborca and New Jersey faunas is modelled after that provided by Onken and Signor (1988) for the Cambrian faunas of eastern California and Nevada. It should aid in biostratigraphic comparisons between the Proterozoic-Cambrian faunas of Mexico, eastern and western United States, and elsewhere. Fossil names used in this report supersede those used in McMenamin (1984) and other sources. A locality register for many of the Mexican fossils can be found in Cooper et al. (1952, 1956), McMenamin (1984), and McMenamin and McMenamin (1990).

Archaeocyathans

Archaeocyathus arborensis (Okulitch, 1954); Archaeocyathidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón, Cerro Calaveras; CR2; MNHN L83075, L83131; Debrenne et al., 1989, p. 158, Pl. 8, figs. 1-2.

Archaeocyathus sp.; Archaeocyathidae; unit 3 of the Puerto Blanco Formation; Proveedora Hills, Cerro Rajón, Cerro Clemente; CR2, 1 of 12/15/82; MNHN L83076-77, L83131; Debrenne et al., 1989, p. 158, Pl. 9, figs. 4-5.

Arrhythmocricus macdamensis (Handfield, 1971); Protocyclocyathellidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón, Cerro Calaveras; CAL6; MNHN L83083-84, L83128; Debrenne et al., 1989, p. 160, 161, Pl. 8, fig. 1c, Pl. 9, fig. 6, text-fig. 11.

Aulocricus arellani Debrenne, 1987; Ethmophyllidae; upper unit 3, lower unit 4 of the Puerto Blanco Formation; Proveedora Hills; 801q, CR2; USNM 111823, 414812; Debrenne et al., 1989, p. 156, Pl. 7, figs. 1-3, text-fig. 10; Debrenne, 1987, p. 271, Pl. 1, figs. 1, 7; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 57, Pl. 11, fig. 5; Cooper et al., 1952, p. 28, Pl. 9, fig. 5. Same specimen as *Ajacicyathus rimouski* (Okulitch, 1943).

Batenevia spinosa Debrenne, 1989; Archaeocyathidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón, Cerro Clemente; CR1, 1 of 12/15/82; MNHN L83092-95; Debrenne et al., 1989, p. 164, 165, Pl. 11, figs. 3-4.

Claruscoscinus sp.; Claruscoscinidae; unit 3 of the Puerto Blanco Formation, upper Buelna formation; Proveedora Hills, Cerro Rajón, Difuntos Hills; MNHN L83101, CR1; 802d, USNM 111820; Debrenne et al., 1989, p. 167-168, Pl. 11, fig. 7; Debrenne, 1987, p. 271, Pl. 1, fig. 5; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 60, Pl. 11, fig. 1A, 2; Cooper et al., 1952, p. 31, Pl. 9, figs. 1A, 2.

Cordilleracyathus meridianus Debrenne, 1989; Ethmophyllidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón; CR2; MNHN L83073-74; Debrenne et al., 1989, p. 154-155, Pl. 7, fig. 5, text-fig. 9.

Dictyocyathus sp. 1; Dictyocyathidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón, Cerro Clemente, Cerro Calaveras; CR1; Debrenne et al., 1989, p. 157, Pl. 7, fig. 6, Pl. 8, fig. 4, Pl. 12, fig. 4. See *Dictyocyathus* sp., Plate 1.1, this report.

Graphoscypbia ramosa Debrenne, 1989; Flindersicyathidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón; CR1; MNHN L83078-79; Debrenne et al., 1989, p. 159, Pl. 8, fig. 3.

Markocyathus clementensis Debrenne, 1989; Archaeocyathidae; unit 3 of the Puerto Blanco Formation; Cerro Clemente; 1 of 12/15/82; MNHN L83096-97; Debrenne et al., 1989, p. 165, 166, Pl. 11, figs. 1-2.

Metaldetes sp. cf. *M. fischeri* (Handfield, 1971); Metacyathidae; unit 3

of the Puerto Blanco Formation; Cerro Rajón, Cerro Calaveras; CR1, CR2, CAL6; Debrenne et al., 1989, p. 162, Pl. 11, fig. 5, 6. See *Metaldetes* sp., Plate 1.1, this report.

Palmericyathellus undatus Debrenne, 1989; Flindersicoscinidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón; CR2; MNHN L83098-99; Debrenne et al., 1989, p. 166, Pl. 12, fig. 3-4.

Palmericyathus americanus (Okulitch, 1952); Sajanocyathidae; upper unit 3 and lower unit 4? of the Puerto Blanco Formation; Proveedora Hills, Cerro Rajón; 801q, CR2.5; USNM 11816a-17b, 414811; Debrenne et al., 1989, p. 153, Pl. 7, fig. 9; Debrenne, 1987, p. 269, Pl. 1, fig. 8; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 59, 60, Pl. 9, figs 3, 4; Cooper et al., 1952, p. 30, 31, Pl. 7, figs. 3, 4. Same as *Ethmophyllum americanum* Okulitch, 1952.

Paranacyathus polycladus Debrenne, 1989; Metacyathidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón, Cerro Clemente, Cerro Calaveras; CR1, CR2, 1 of 12/15/82; MNHN L83086-92, L83132; Debrenne et al., 1989, p. 163, 164, Pl. 10, figs. 1-6, Figs. 12, 13.

Parethmophyllum cooperi (Okulitch, 1952); Ethmophyllidae; unit 3? and lower unit 4? of the Puerto Blanco Formation; Proveedora Hills; 801y, 801q; USNM 111814-14a, 111817a-b, 111818a-c; Debrenne et al., 1989, p. 154, Pl. 7, fig. 6; Debrenne, 1987, p. 270, Pl. 1, figs. 2-4; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 57-59, Pl. 10, figs. 3-5, Pl. 9, figs. 1, 2; Pl. 11, fig. 4; Cooper et al., 1952, p. 28-30, Pl. 8, figs. 3-5, Pl. 7, figs. 1, 2, Pl. 9, fig. 4. Same as *Syringocnema*? sp.; *Ethmophyllum whitneyi* Meek, 1868; and *Ethmophyllum cooperi* Okulitch, 1952.

Protopharetra sp.; Protopharetridae; unit 3 of the Puerto Blanco Formation; Cerro Clemente, Cerro Rajón, Cerro Calaveras; CR1, 1 of 12/15/82; Debrenne et al., 1989, p. 157, Pl. 8, fig. 4.

Pycnoidocyathus eminetus Debrenne, 1989; Flindersicyathidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón; CR2; MNHN L83081; Debrenne et al., 1989, p. 160, Pl. 9, figs. 1-3.

Representative of the Order Metacyathina; upper Buelna Formation; Difuntos Hills; 802d; USNM 111821; Debrenne, 1987, p. 269; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 63, Pl. 11, fig. 3; Cooper et al., 1952, p. 33, Pl. 9, fig. 3. Same as *Cambrocyathus* aff. *C. occidentalis* Okulitch, 1943.

Representative of the Suborder Archaeocyathina; upper unit 3 and lower unit 4? of the Puerto Blanco Formation, upper Buelna Formation; Proveedora Hills, Difuntos Hills; 801y, 802d; USNM 111824; Debrenne, 1987, p. 268, 269; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 61, 62, Pl. 12, fig. 1, Pl. 11, fig. 1B; Cooper et al., 1952, p. 31-33, Pl. 10, fig. 1, Pl. 9, fig. 1B. Same as *Archaeocyathus yavorskii* (Vologdin, 1931) and *Protopharetra* sp.

Retilamina sp.; order and family uncertain; unit 3 of the Puerto Blanco Formation; Cerro Rajón; CR2; MNHN L83102; Debrenne et al., 1989, p. 108, Pl. 12, fig. 2.

Rotundocyathus pusillus? Debrenne, 1989; Ajacicyathidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón; CR1, CR2; MNHN L83060-62; Debrenne et al., 1989, p. 152, Pl. 7, fig. 4, Pl. 8, fig. 16.

Stevocyathus elictus Debrenne, 1989; Flindersicoscinidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón; CR2; MNHN L83100; Debrenne et al., 1989, p. 167, Pl. 12, fig. 1.

Tumulocyathellus minor Debrenne, 1989; Tumulocyathidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón area; CR2; MNHN L83063-64; Debrenne et al., 1989, p. 152, 153, Pl. 7, figs. 7, 8.

Young stage of Ajacicyathida, probably *Parethmophyllum cooperi* (Okulitch, 1952); Suborder Ajacicyathina; unit 3 and lower unit 4 of the Puerto Blanco Formation; Proveedora Hills; 801y; USNM

111815; Debrenne, 1987, p. 269, Pl. 1, fig. 6; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 56, Pl. 9, fig. 5, 6, Pl. 11, fig. 4; Cooper et al., 1952, p. 28, Pl. 7, fig. 5, 6, Pl. 9, fig. 4. Same as *Ajacicyathus nevadensis* (Okulitch, 1935).

Brachiopods

Acrothele concava Cooper, 1952; Acrothelidae; upper Arrojos Formation; Arrojos Hills; 800f; USNM 116035a-f; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 78, 79, Pl. 14A, figs. 1-6; Cooper et al., 1952, p. 44, 45, Pl. 12A, figs. 1-6.

Acrothele sp.; Acrothelidae; Arrojos Formation, lower Tren Formation; Stewart et al., 1984, p. 19.

Alisina mexicana (Cooper, 1952); Obolellidae; upper unit 3 and lower unit 4 of the Puerto Blanco Formation; Proveedora Hills, Cañedo Hill; 801b, 812b; USNM 116041a-f, 116051a-f, 116056a-c; Stewart et al., 1984, p. 19; Rowell, 1962, p. 141, 142; Cooper et al., 1956, p. 74, 75, Pl. 14D, figs. 20-31; Cooper et al., 1952, p. 41, 42, Pl. 12D, figs. 20-31.

Class, order, and genus indeterminate; unit 3 of the Puerto Blanco Formation; sample 7 of 12/17/82; IGM 3625; McMenamin, 1984, p. 61, 62, Pl. 7, fig. 5. Possibly an internal mold of a brachiopod.

Dictyonina minutipuncta Cooper, 1952; Paterinidae; upper Arrojos Formation; Arrojos Hills; 800f; USNM 116045a-h; Stewart et al., 1984, p. 19; Cooper et al. 1956, p. 72-73, Pl. 13A, figs. 1-6; Cooper et al., 1952, p. 40, Pl. 11A, figs. 1-6.

Dictyonina sp.; Paterinidae; Arrojos Formation, lower Tren Formation; Arrojos Hills; 800g; USNM 116044a, d, e.; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 73, Pl. 14B, figs. 7-9; Cooper et al., 1952, p. 41, Pl. 12B, figs. 7-9.

Diraphora arrojosensis Cooper, 1952; Eoorthidae; middle and upper Arrojos Formation; Arrojos Hills, Proveedora Hills; 800c, 801n, 801o; USNM 116042a-j; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 82-84, Pl. 15E, figs. 15-25; Cooper et al., 1952, p. 47, 48, Pl. 13E, figs. 15-25.

Kutorgina sp.; Kutorginidae; lower unit 2 of the Puerto Blanco Formation; Cerro Rajón area; sample 4 of 12/17/82; IGM 3647-48; McMenamin and McMenamin, 1990, p. 72, Fig. 4.19C; McMenamin, 1984, p. 60, 61, Pl. 16, figs. 5, 6; Stewart et al., 1984, p. 19 (as "possible nususiids").

Lingulella proveedorensis Cooper, 1952; Obolidae; upper half unit 3 and lower half unit 4 of the Puerto Blanco Formation; 801b; USNM 116039a-d-40a-c; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 68-70, Pl. 15, fig. 4-6; Cooper et al., 1952, p. 37, 38, Pl. 13B, figs. 4-6.

Lingulella sp.; Obolidae; upper half of unit 2, unit 3, unit 4 of the Puerto Blanco Formation; Cerro Clemente, Cerro Rajón area; samples 1 of 12/15/82, MM-82-49; IGM 3614[35-36]; McMenamin and McMenamin, 1990, p. 72, 178, fig 4.19A; McMenamin, 1984, p. 52-53, Pl. 18, fig. 1-3; Stewart et al., 1984, p. 19.

Linnarssonina arellanoi (Cooper, 1952); Acrotretidae; lower Tren Formation; Arrojos Hills; 800g; USNM 116058a-g; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 77, Pl. 15C, figs. 7-12; Cooper et al., 1952, p. 43, 44, Pl. 13, figs. 7-12.

Linnarssonina rara (Cooper, 1952); Acrotretidae; base of Arrojos Formation; Arrojos Hills; 800a; USNM 116057a-d, 116059a-g; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 76, 77, Pl. 14C, figs. 10-19; Cooper et al., 1952, p. 42, 43, Pl. 12C, figs. 10-19.

Mickwitzia sp.; Mickwitziidae; unit 2 and upper unit 3 of the Puerto Blanco Formation; Cerro Rajón area, Proveedora Hills

- (Problematicum I of Cooper et al. (1952, 1956)); sample 5.5+ of 12/17/82; IGM 3614[33] and 3614[34]; 801b; USNM 115660; McMenamin and McMenamin, 1990, p. 72, Fig. 4.19B (IGM 3614[34] *not* IGM 3614[33] as erroneously listed on p. 178), p. 119, Fig. 7.6 (IGM 3614[33]); McMenamin, 1986, p. 179, 180, Figs. 3, 4 (IGM 3614[33]), Fig. 5 (IGM 3614[34]); McMenamin, 1984, p. 56-58, Pl. 17, figs. 1-6, Pl. 18, fig. 4; Cooper et al., 1956 (as Problematicum I), p. 124, 125, Pl. 17, figs. 1, 2; Cooper et al., 1952 (as Problematicum I), p. 81, Pl. 15, figs. 1, 2.
- Micromitra* sp.; Paterinidae; basal Arrojos Formation; Arrojos Hills; 800a; USNM 116046a-d; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 71, 72, Pl. 15A, figs. 1-3; Cooper et al., 1952, p. 39, 40, Pl. 13A, figs. 1-3.
- Nisusia* sp.; Nisusiidae; basal Arrojos Formation; Proveedora Hills; 801h; USNM 116037b-c; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 80-81, Pl. 15F, figs. 26, 27; Cooper et al., 1952, p. 45, 46, Pl. 13F, figs. 26, 27.
- Paterina* sp.; Paterinidae; upper Buelna Formation, unit 2 of the Puerto Blanco Formation; Buelna Hills, Cerro Rajón area; 807c, sample 4 of 12/17/82; USNM 116050a-b, IGM 3614[30-32]; McMenamin and McMenamin, 1990, p. 72, Fig. 4.19D; McMenamin, 1984, p. 54, 55, Pl. 16, figs. 1-4, Pl. 18, fig. 5; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 70, 71, Pl. 13B, figs. 7, 8; Cooper et al., 1952, p. 38, 39, Pl. 11B, figs. 7, 8.
- Wimanella* sp.; Eoorthidae; middle and upper Arrojos Formation; Proveedora Hills; 801i; USNM 116054-55a; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 81, 82, Pl. 15D, fig. 13, 14; Cooper et al., 1952, p. 47, Pl. 13D, figs. 13, 14.
- Hyoliths*
- Allatheca?* sp. cf. *A.?* *buelna* (Lochman, 1952); Allathecidae; units 2 and 3 of the Puerto Blanco Formation; sample 5.5+ of 12/17/82; IGM 3614[20]; McMenamin, 1984, p. 44, Pl. 14, fig. 1.
- Genus and species indeterminate C; Allathecidae; unit 2 of the Puerto Blanco Formation; sample 5.5+ of 12/17/82; IGM 3614[25]; McMenamin, 1984, p. 45, Pl. 14, fig. 7.
- Hyolithes sonora* Lochman, 1952; Hyolithidae; Arrojos Formation; Arrojos Hills, Proveedora Hills; 800a, 800c, 801i, 801n, 801o; USNM 115902-10; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 161, 162, Pl. 29, figs. 17-25; Cooper et al., 1952, p. 113, 114, Pl. 27, figs. 17-25.
- Hyolithes* sp.; Hyolithidae; Buelna Formation, Arrojos Formation, unit 2 of the Puerto Blanco Formation; sample 5.5+ of 12/17/82; IGM 3646, 3614[21]; McMenamin, 1984, p. 47, Pl. 14, figs. 2, 3; Stewart et al., 1984, p. 19.
- Hyolithes* sp. aff. *H. princeps* Billings, 1872; Hyolithidae; upper half unit 3 and lower half unit 4 of the Puerto Blanco Formation; Proveedora Hills; 801b, 801g; USNM 11564-66a, 115667; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 125-127, Pl. 17, figs. 9-13; Cooper et al., 1952, p. 82, 83, Pl. 15, figs. 9-13.
- Hyolithes whitei* Resser, 1938, Hyolithidae; Buelna Formation; Buelna Hills, Prieto Hill; 807b, 809a; USNM 115669-71a, b; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 127-128, Pl. 18, figs. 2-6; Cooper et al., 1952, p. 83, 84, Pl. 16, figs. 2-6.
- Orthotheca buelna* Lochman, 1952; Orthothecidae; Buelna Formation; Buelna Hills; 807b; USNM 115662a-b; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 128, Pl. 17, figs. 4, 5; Cooper et al., 1952, p. 84, Pl. 15, figs. 4, 5.
- Paragloborilus mirus?* Qian, 1977; Allathecidae; units 2 and 3 of the Puerto Blanco Formation; Cerro Rajón area; samples 5.5+ of 12/17/82, MM-82-51; IGM 3614[24, 28]; McMenamin, 1984, p. 42, 43, Pl. 14, fig. 6, Pl. 15, fig. 5.
- Coelosclerotophorans*
- Chancelloria eros* Walcott, 1920; Chancelloriidae; Puerto Blanco Formation, Arrojos Formation; Arrojos Hills, Proveedora Hills; 800a, 800c, 801n; USNM 115912-16, 115918, 115919a; Stewart et al., 1984, p. 19 (incorrectly shown occurring in the Puerto Blanco Formation); Cooper et al., 1956, p. 158-161, Pl. 30, figs. 1-7; Cooper et al., 1952, p. 110, 111, Pl. 28, figs. 1-7.
- Chancelloria* spp.; Chancelloriidae; units 2 and 3 of the Puerto Blanco Formation; Arrojos Hills, Cerro Rajón area, Sierra del Viejo; samples 4, 5.5, 5.5+, 7, and 7c of 12/17/82, 1 and 2 of 12/15/82, MM-82-49, MM-82-51, MM82-83; IGM 3614[12], 3643; 800f, 800b; McMenamin, 1984, p. 87, 88, Pl. 12, figs. 5, 7.
- Calcareous problematica*
- Cambrotubulus* sp. cf. *C. decurvatus* Missarzhevskii in Rozanov et al., 1969; incertae sedis; unit 1 of La Ciénega Formation; samples MM-82-69 and 1 of 12/13/82; IGM 3614[2], 3617; McMenamin, 1985, p. 1421, Figs. 5.1, 5.4; McMenamin, 1984, p. 77, 78, Pl. 3, fig. 1.4. The possibility exists that this represents a dolomitized burrow rather than a shelly fossil; similar specimens that branch have been recovered from acetic acid maceration of calcareous sedimentary rocks at the same level in the La Ciénega Formation.
- Hyolithellus micans* Billings, 1872; Hyolithellidae; unit 3 of the Puerto Blanco Formation; sample MM-82-49; IGM 3614[12]; McMenamin, 1984, p. 89, Pl. 12, figs. 3, 4.
- Hyolithellus* sp.; Hyolithellidae; units 2, 3 and 4 of the Puerto Blanco Formation; Cerro Rajón, Cerro Clemente; samples MM-82-49, MM-82-54, 4, 7c, 5.5 and 5.5+ of 12/17/82, 1, 2, and 6.5 of 12/15/82; IGM 3614[14, 29]; McMenamin and McMenamin, 1990, p. 53, 120, Figs. 4.5, 7.8; McMenamin, 1987b, p. 100, upper figure; McMenamin, 1984, p. 89-91, Pl. 12, figs. 1, 2, 6, Pl. 15, fig. 6; Stewart et al., 1984, p. 19.
- Problematicum II of Cooper et al. (1952, 1956); upper unit 3, Puerto Blanco Formation; Proveedora Hills; 801b; USNM 115661; Cooper et al., 1956, p. 124, 125, Pl. 17, fig. 3; Cooper et al., 1952, p. 81, Pl. 15, fig. 3. MASM has seen this specimen; it is possibly a specimen of the ?monoplacophoran *Proplina* with a very large rate of whorl increase or, alternatively, the "anterior plate" from a halkieriid scleritome.
- Sinotubulites cienegensis* McMenamin, 1985; Cloudinidae; unit 1 of La Ciénega Formation; western Cerro Clemente, Cerros Calaveras, Cerro Rajón area, Cerro Pitiquito; samples MM-82-41, MM-82-41a, MM-82-68, MM-82-81, MM-82-84 and 1 of 12/13/82; IGM 3490-91, 3608, 3610-14[1], 3615-16, 3618; McMenamin, 1989, p. 78, Fig. 4.4; McMenamin, 1985, p. 1417-1420, Figs. 3.2-3.6, 4.1, 4.2, 4.4-4.7, 5.2, 5.5, 5.6 ("orthotheid hyolith" [p. 1423, Fig. 5.3, sample MM-82-41a, IGM 3616] is now known to be a multi-walled specimen of *Sinotubulites cienegensis*; S.W.F. Grant, personal commun., 1989); McMenamin, 1984, p. 40, 75-77, Pl. 1, figs. 2-6, Pl. 2, figs. 1, 2, 4-7, Pl. 3, figs. 2, 3, 5, 6; Stewart et al., 1984, p. 19 (as ?*Sinotubulites* sp.), p. 21, Fig. 12; McMenamin et al., 1983, p. 229, Fig. 3a-d; Signor et al., 1983, p. 416, Fig. 3e-h.
- Tommatiids*
- Lapworthella filigrana* Conway Morris and Fritz, 1984;

Lapworthellidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón area, Cerro Clemente; samples 7c of 12/17/82, 2 of 12/15/82; IGM 3642, 3614[3-5, 6, 9-11]; McMenamin and McMenamin, 1990, p. 57, Fig. 4.8; McMenamin, 1988, p. 205, Fig. 1; McMenamin, 1984, p. 85, 86, Pl. 10, figs. 1-6; Pl. 11, figs. 1-5. See Plate 1.6, this report.

Phosphatic problematica

Genus and species indeterminate D; incertae sedis; unit 2 of the Puerto Blanco Formation; Cerro Rajón area; samples 5.5, 5.5+ of 12/17/82; IGM 3614[26-27]; McMenamin, 1984, p. 81-83, Pl. 15, figs. 1, 3, 4.

Microdictyon sp.; incertae sedis; middle and upper unit 2, lower unit 3 of the Puerto Blanco Formation; Cerro Rajón area, Cerro Clemente; samples 5.5, 5.5+, and 7c of 12/17/82, MM-82-49, 1 and 2 of 12/15/82; McMenamin and McMenamin, 1990, p. 80, Fig. 4.28; McMenamin, 1984, p. 80, 81, Pl. 13, figs. 1, 2, 4; Stewart et al., 1984, p. 19.

Paiutitubulites sp.; Paiutitubulitidae; unit 3 of the Puerto Blanco Formation; Cerro Clemente; sample 1 of 12/15/82. See Plate 1.3, this report.

Problematicum I of Cooper et al. (1952, 1956); see *Mickwitzia* sp.

Problematicum III of Cooper et al. (1952, 1956); Arrojitos Formation, *Mexicaspis* bed, approximately 95 m above base of section; Arrojitos Hills; 800d; USNM 115920-21; Cooper et al., 1956, p. 157, 158, Pl. 30, figs. 8-11; Cooper et al., 1952, p. 109, 110, Pl. 28, figs. 8-11. Possible phosphatic operculum or chondrophore float?

Agmatans

Salterella maccullochi (Murchison, 1859); Salterellidae; upper half Buelna Formation, Puerto Blanco Formation; Buelna Hills, Prieto Hills, Proveedora Hills; 800, 801b, 801e, 801g, 801q', 801t, 807, 807b, 807f-g, 809a, 809d; Stewart et al., 1984, p. 19; Cooper et al., 1956 (as *S. mexicana* Lochman, 1952), p. 129-131, Pl. 17, fig. 14, Pl. 18, figs. 7-11, Pl. 19, figs. 1-5; Cooper et al., 1952 (as *S. mexicana* Lochman, 1952), p. 85-87, Pl. 15, fig. 14, Pl. 16, figs. 7-11, Pl. 17, figs. 1-5. Yochelson (1981, p. 246) stated, "probably *S. mexicana* Lochman (1952) is...synonymous with *S. maccullochi*."

Salterella sp.; Salterellidae; Buelna Formation, Cerro Prieto Formation; Cañedo Hill, Proveedora Hills, Cerro Rajón area; samples MM-82-57, MM-82-56; 812a; USNM 115679; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 132, 133, Pl. 19, fig. 6, 7; Cooper et al., 1952, p. 88, Pl. 17, fig. 6, 7. According to Cooper et al. (1956), *Salterella* (as *Salterella* sp. on p. 42 or as *S. mexicana* Lochman, 1952 on p. 131) ranges down into unit 3 of the Puerto Blanco Formation (locality 801b). This occurrence in the Puerto Blanco Formation, if it truly belongs to the *Nevadella* Zone, as our correlations suggest, would represent an anomalously low stratigraphic occurrence for this genus (see Yochelson, 1981).

Salterella sp. cf. *S. pulchella* Billings, 1861; Salterellidae; upper Buelna Formation; Prieto Hill; 809a; USNM 115668; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 131-133, Pl. 18, fig. 1; Cooper et al., 1952, p. 87, 88, Pl. 16, fig. 1.

Monoplacophorans

Bemella pauper (Billings, 1872); Helcionellidae; middle unit 2 of the Puerto Blanco Formation; sample 5.5 of 12/17/82; IGM 3614[16, 18]; McMenamin, 1987a; McMenamin, 1984, p. 48-50, Pl. 13, fig. 3-5; "helcionellid" of Stewart et al., 1984, p. 19.

Bemella sp.; Helcionellidae; units 2 and 3 of the Puerto Blanco

Formation; Cerro Rajón, Cerro Clemente; samples 5.5 of 12/17/82 and 1 of 12/15/82; McMenamin and McMenamin, 1990, p. 119, Fig. 7.7.

Helcionella sp. indet.; Helcionellidae; middle Arrojitos Formation, Arrojitos Hills; 800c; USNM 115936; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 162, 163, Pl. 30, figs. 23-25; Cooper et al., 1952, p. 114, Pl. 28, figs. 23-25.

Pelagiella sp.; Pelagiellidae; units 2 and 3 of the Puerto Blanco Formation, Buelna Formation; Cerro Rajón area, Sierra del Viejo; samples 5.5+ and 7c of 12/17/82, MM-82-83; IGM 3614[19], 3644; McMenamin and McMenamin, 1990, p. 74, Fig. 4.21; McMenamin 1984, p. 50, 51, Pl. 12, fig. 8, Pl. 13, fig. 6; "pelagiellid gastropods" of Stewart et al., 1984, p. 19.

Scenella sp. cf. *S. reticulata* Billings, 1872; Scenellidae; upper Buelna Formation; Prieto Hill; 809a; USNM 115663; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 128-129, Pl. 17, figs. 6-8; Cooper et al., 1952, p. 85, Pl. 15, figs. 6-8.

Trilobites

Albertella proveedora Lochman, 1952; Zacanthoidae; middle Arrojitos Formation; Proveedora Hills; 801i, 801k, 802a; USNM 115776-84; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 190-192, Pl. 25, figs. 1-9; Cooper et al., 1952, p. 137-139, Pl. 23, figs. 1-9; *Albertella* sp. aff. *A. proveedora* Lochman, 1952 of Lochman (1952; 802a; USNM 115784) is considered here to be conspecific with *Albertella proveedora*.

Alokistocare althea Walcott, 1916; Alokistocaridae; upper Arrojitos Formation; Proveedora Hills; 801o; USNM 115887-115892; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 163-165, Pl. 29, figs. 3-8; Cooper et al., 1952, p. 114-116, Pl. 27, figs. 3-8.

Alokistocare mexicana Lochman, 1952; Alokistocaridae; middle and upper Arrojitos Formation; Arrojitos Hills, Proveedora Hills; 800c, 801n; USNM 115884, 115885a, 115886; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 167-169, Pl. 29, figs. 1, 2; Cooper et al., 1952, p. 118, 119, Pl. 27, figs. 1, 2.

Alokistocare modestum Lochman, 1952; Alokistocaridae; upper Arrojitos Formation; Proveedora Hills; 801n; USNM 115898-99, 115900-01a-d; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 165, 166, Pl. 29, figs. 11-16; Cooper et al., 1952, p. 116, 117, Pl. 27, figs. 11-16.

Alokistocare sp. cf. *A. modestum* Lochman, 1952; Alokistocaridae; upper Arrojitos Formation; Arrojitos Hills; 800a; USNM 115894-95; Stewart et al., 1984, p. 18; Cooper et al., 1956 [*Alokistocare*(?)], Pl. 29, figs. 9, 10; Cooper et al., 1952, p. 117, 118, Pl. 27, figs. 9, 10.

Amecephalus arrojitosensis (Lochman, 1952); Alokistocaridae; lower Arrojitos Formation; Proveedora Hills; 801h; USNM 115753-57; Stewart et al., 1984, p. 18 (misspelled on the chart); Cooper et al., 1956, p. 198-200, Pl. 23, figs. 29-34; Lochman, 1953, p. 486; Cooper et al., 1952, p. 157, 158, Pl. 21, figs. 29-34.

Antagmus buttsi (Resser, 1939); Antagminae; upper Buelna Formation; Prieto Hill; 809a; USNM 115736-39; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 147-149, Pl. 23, figs. 15-21; Cooper et al., 1952, p. 101-103, Pl. 21, figs. 15-21.

Antagmus solitarius Lochman, 1952; Antagminae; upper Buelna Formation; Prieto Hill; 809a; USNM 115740-41; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 149, 150, Pl. 23, figs. 8-11; Cooper et al., 1952, p. 103, 104, Pl. 21, figs. 8-11.

Arellanella caborcana Lochman, 1948; Alokistocaridae; lower Arrojitos Formation; Arrojitos Hills; 800a; USNM 115961-65; Stewart et al.,

- 1984, p. 18; Cooper et al., 1956, p. 200, 201, Pl. 31, figs. 23-29; Cooper et al., 1952, p. 144, 145, Pl. 29, figs. 23-29.
- Arellanella sonora* Lochman, 1952; Alokistocaridae; upper and ?middle Arrojos Formation; Arrojos Hills; 800a, 800b, USNM 115953-57, 115958-59; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 202, 203, Pl. 31, figs. 15-19; Cooper et al., 1952, p. 146, 147, Pl. 29, figs. 15-22.
- Athabaskia bela* (Walcott, 1916); Ptarmiganidae; middle and upper Arrojos Formation; Arrojos Hills, Proveedora Hills; 800c, 801n; USNM 115941-43, 115945-48; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 177-179, Pl. 31, figs. 1-10; Cooper et al., 1952, p. 128-130, Pl. 29, figs. 1-10.
- Athabaskia minor* (Resser, 1938); Ptarmiganidae; Arrojos Formation; Arrojos Hills; 800g; USNM 115987-89; Stewart et al., 1984, p. 18 (incorrectly placed in Tren Formation); Cooper et al., 1956, p. 179-181, Pl. 33, figs. 1-3; Cooper et al., 1952, p. 130, 131, Pl. 31, figs. 1-3.
- Bonnina sonora* Lochman, 1952; Corynexochidae; upper Buelna Formation; Prieto Hill; 809a; USNM 115736-39; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 145-147, Pl. 23, figs. 1-7; Cooper et al., 1952, p. 99-101, Pl. 21, figs. 1-7.
- Caborcella arrojosensis* Lochman, 1948; Ptychopariidae; Arrojos Formation; Arrojos Hills; 800c; USNM 115950-52; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 203, 204, Pl. 31, figs. 11-14; Cooper et al., 1952, p. 147, 148, Pl. 29, figs. 11-14; Lochman, 1948, p. 461, Pl. 70, figs. 19-21.
- cf. *Fallotaspis* Hupé, 1953; Olenellidae; unit 2 of the Puerto Blanco Formation; Cerro Rajón area, Cerro Clemente; samples 6.5 of 12/19/82, 5 of 3/20/90; IGM 3652; McMenamin 1987a, p. 743, Fig. 5.4; Stewart et al., 1984, p. 18; McMenamin, 1984, p. 63, 64, Pl. 19, fig. 4; McMenamin, 1983, p. 80-81, Figs. 3A, 4B (incorrectly listed in caption as 4A).
- Genus and species indeterminate E; Olenellidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón area; specimen 7c of 12/17/82; IGM 3656; McMenamin, 1987a, p. 747, Fig. 6.2; McMenamin, 1984, p. 69, 70, Pl. 20, fig. 2.
- Genus and species undetermined 1 of Cooper et al. (1952, 1956); Buelna Formation; Prieto Hill; 809a; USNM 115742; Cooper et al., 1956, p. 155-157, Pl. 23, fig. 13, 14; Cooper et al., 1952, p. 108, 109, Pl. 21, fig. 13, 14.
- Genus and species undetermined 2 of Cooper et al. (1952, 1956); Arrojos Formation; Proveedora Hills; 801h; USNM 115850a; Cooper et al., 1956, p. 215, 216, Pl. 27, fig. 22; Cooper et al., 1952, p. 158, 159, Pl. 25, fig. 22.
- Genus and species undetermined 3 of Cooper et al. (1952, 1956); Tren Formation; Arrojos Hills; 800h; USNM 115994; Cooper et al., 1956, p. 216, Pl. 33, fig. 7; Cooper et al., 1952, p. 159, Pl. 31, fig. 7.
- Genus and species undetermined 4 of Cooper et al. (1956) (=“Cf. Middle Cambrian trilobites” of Cooper et al. [1952]); Formation unknown, possibly Middle Cambrian; Lista Blanca, south side of Magdalena River; 811a; USNM 115990; Cooper et al., 1956, p. 216, Pl. 33, fig. 4; Cooper et al., 1952, p. 159, Pl. 31, fig. 4.
- Glossopleura leona* Lochman, 1952; Ptarmiganidae; middle and upper Arrojos Formation; Difuntos Hills, Proveedora Hills; 802b, 802c, 801m, 801n; USNM 115830-39, 115841-49; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 185-187, Pl. 27, figs. 1-21; Cooper et al., 1952, p. 135, 136, Pl. 25, figs. 1-21.
- Glossopleura* sp.; Ptarmiganidae; Arrojos Formation; Arrojos Hills, Proveedora Hills; 800e, 800e', 800f, 801m'; USNM 115995-96, 116333-36; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 187-188, Pl. 33, figs. 8-14; Cooper et al., 1952, p. 137, Pl. 31, figs. 8-14.
- Inglefieldia imperfecta* Lochman, 1952; family indet.; upper Arrojos Formation; Arrojos Hills; 800e, 800e', 800f; USNM 115966-76; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 204-206, Pl. 32, figs. 1-10; Cooper et al., 1952, p. 148-150, Pl. 30, figs. 1-10.
- Inglefieldia* sp. cf. *I. imperfecta* Lochman, 1952; family indet.; Arrojos Formation; Arrojos Hills; 800g; USNM 115977; Stewart et al., 1984, p. 18 (incorrectly placed in Tren Formation); Cooper et al., 1956, p. 206, 207; Cooper et al., 1952, p. 150.
- Judomia orbis* McMenamin, 1987a; Olenellidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón area, Cerro Clemente; samples 7 of 12/17/82, 2 of 3/20/90; IGM 3649, 3651, 3659; McMenamin, 1987a, p. 745-747, Figs. 4, 5.1, 25.3, 6.7, 6.8; Stewart et al., 1984, p. 18; McMenamin, 1984, p. 68-69, Pl. 19, figs. 1, 3, Pl. 20, figs. 7-8; McMenamin, 1983, p. 79, Figs. 3B, 4A (incorrectly listed in caption as 4B). *Judomia orbis*=cf. *Judomia* in Stewart et al. (1984) and McMenamin (1983).
- Kistocare corbini* Lochman, 1948; Alokistocaridae; middle and upper Arrojos Formation; Arrojos Hills, Proveedora Hills; 800c, 801n, USNM 115923-30; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 169-170, Pl. 30, figs. 12-22; Cooper et al., 1952, p. 119, 120, Pl. 28, figs. 12-22; Lochman, 1948, p. 463, Pl. 70, figs. 1-6.
- Kistocare tontoensis* (Resser, 1945); Alokistocaridae; lower Arrojos Formation; Arrojos Hills; 800a; USNM 115937-40; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 170-172, Pl. 30, figs. 26-31; Cooper et al., 1952, p. 121, 122, Pl. 28, figs. 26-31.
- Kochaspis* sp. aff. *K. celer* (Walcott, 1917); see “*Ptychoparia*” sp. aff. *P. clusia* Walcott, 1917.
- Kochaspis cooperi* Lochman, 1952; Crepicephalidae; middle Arrojos Formation; Proveedora Hills; 801k; USNM 115853-55; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 172, 173, Pl. 27, figs. 33, 34; Lochman, 1953, p. 486; Cooper et al., 1952, p. 122, 123, Pl. 25, figs. 33, 34.
- Kochaspis*? sp.; Crepicephalidae; lower and middle Arrojos Formation; Proveedora Hills; 801h, 801i; USNM 115851, 115852a; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 173, 174, Pl. 27, figs. 23, 24; Cooper et al., 1952, p. 125, Pl. 25, figs. 23, 24.
- Kootenia exilaxata* (Deiss, 1939); Kootenidae; middle and upper Arrojos Formation; Arrojos Hills, Proveedora Hills; 800c, 801n; USNM 115869-78, 115880-82; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 174-177, Pl. 28, figs. 1-20; Cooper et al., 1952, p. 125-128, Pl. 26, figs. 1-20.
- Laudonia mexicana* (Lochman, 1952); Olenellidae; lower half of unit 4 of the Puerto Blanco Formation; Proveedora Hills; 801c; USNM 115681-84; McMenamin, 1987a, p. 738-739; Stewart et al., 1984, p. 18 (as *Laudonia* sp.), 19 (as *Wanneria mexicana prima* Lochman, 1952; the range is incorrectly shown as occurring at the base of unit 4 of the Puerto Blanco Formation; the actual position is between about 25-50 m above the base of the unit; see Cooper et al., 1952, their Fig. 5, p. 6); Fritz, 1975, p. 534, 536; Cooper et al., 1956, p. 141-144, Pl. 20, figs. 1-3; Cooper et al., 1952, p. 96-98, Pl. 18, figs. 1-3.
- Mexicaspis difuntosensis* Lochman, 1952; Zacantheidae; Arrojos Formation; Difuntos Hills; 802a, b; USNM 115766-72, 115774-75; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 193-195, Pl. 24, figs. 10-23; Cooper et al., 1952, p. 139-141, Pl. 22, figs. 10-23.
- Mexicaspis stenopyge* Lochman, 1948; Zacantheidae; middle Arrojos Formation; Arrojos Hills, Proveedora Hills; 800d, 801l, 801ka;

USNM 115785-94, 115796, 115798-99; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 195-197, Pl. 25, figs. 10-27; Cooper et al., 1952, p. 141-143, Pl. 23, figs. 10-27; Lochman, 1948, p. 455, Pl. 69, figs. 1-11.

Mexicella mexicana Lochman, 1948; Alokistocaridae; middle Arrojos Formation; Arrojos Hills, Proveedora Hills, Difuntos Hills; 800d, 801j, 801k, 801ka, 801l, 802a, 802b; USNM 115800-05, 115807-15, 115817-22, 115829; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 207-210, Pl. 26, figs. 1-25; Cooper et al., 1952, p. 150-152, Pl. 24, figs. 1-25; Lochman, 1948, p. 457, Pl. 69, figs. 12-22.

Nevadia ovalis McMenamin, 1987a; Olenellidae; unit 3 of the Puerto Blanco Formation; Cerro Rajón area; sample 7 of 12/17/82; IGM 3655; McMenamin, 1987a, p. 744, 745, Figs. 3, 5.2, 5.5, 5.6, 6.1, 6.3, 6.4, 6.6; Stewart et al., 1984, p. 18; McMenamin, 1984, p. 65-67, Pl. 19, figs. 2, 5, 6, Pl. 20, figs. 1, 3, 4, 6; McMenamin, 1983, p. 79, Figs. 3D, 4C. *Nevadia ovalis*=cf. *Nevadia* in Stewart et al. (1984) and McMenamin (1983).

Olenellus (Fremontia) fremonti Walcott, 1910; Olenellidae; middle and upper Buelna Formation; Prieto Hill; 809a; USNM 115685-86; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 136-139, Pl. 20, figs. 4, 5; Cooper et al., 1952, p. 91-94, Pl. 18, figs. 4, 5.

Olenellus puertoblancoensis (Lochman, 1952); Olenellidae; Buelna Formation; Proveedora Hills, Buelna Hills, Prieto Hill; 801e, 801f, 807c, 809a, 807b, 807e; USNM 115703, 115705a-710; Stewart et al., 1984, p. 18; Fritz, 1975, p. 538; Cooper et al., 1956, p. 139-141, Pl. 21, figs. 9-16; Cooper et al., 1952, p. 94, 95, Pl. 19, figs. 9-16 (as *Paedeumias puertoblancoensis*).

Olenellus sp.; Olenellidae; upper unit 3 and lower unit 4 of the Puerto Blanco Formation; Proveedora Hills; 801b; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 139; Cooper et al., 1952, p. 94.

Olenellus truemani Walcott, 1913; Olenellidae; Buelna Formation; Buelna Hills; 807b, 807c, 807e; USNM 115687, 115689-92; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 133-136, Pl. 20, figs. 6-12; Cooper et al., 1952, p. 89-91, Pl. 18, figs. 6-12.

Onchocephalus buelnaensis Lochman, 1952; Ptychopariidae; middle and upper Buelna Formation; Proveedora Hills, Buelna Hills, Prieto Hill; 809a, 807c, 801f; USNM 115724-35; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 151, 152, Pl. 22, figs. 18, 29; Cooper et al., 1952, p. 104, 105, Pl. 20, figs. 18-29.

Onchocephalus mexicanus Lochman, 1952; Ptychopariidae; middle and upper Buelna Formation; Proveedora Hills, Buelna Hills, Prieto Hill; 809a-b, 807c, 801f; USNM 115713-23; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 153, 154, Pl. 22, figs. 6-17; Cooper et al., 1952, p. 105-107, Pl. 20, figs. 6-17.

Pachyaspidis deborra Lochman, 1952; Ptychopariidae; upper Arrojos Formation; Difuntos Hills; 802c, USNM 115856-60; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 210, 211, Pl. 27, figs. 25-32; Cooper et al., 1952, p. 152, 153, Pl. 25, figs. 25-32.

Pachyaspidis isabella Lochman, 1952; Alokistocaridae; middle and upper Arrojos Formation; Proveedora Hills; 801m-n; USNM 115861-66, 115868; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 211, 212, Pl. 28, figs. 21-29; Cooper et al., 1952, p. 154, 155, Pl. 26, figs. 21-29.

Pachyaspidis sp.; Alokistocaridae; middle and upper Arrojos Formation; Difuntos Hills; 802a; USNM 115823; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 213, Pl. 26, fig. 26; Cooper et al., 1952, p. 155, Pl. 24, fig. 26.

Parehmania sp.; Alokistocaridae; upper Tren Formation; Arrojos Hills; 800h; USNM 115992-93; Stewart et al., 1984, p. 18; Cooper et al.,

1956, p. 213, 214, Pl. 33, figs. 5, 6; Cooper et al., 1952, p. 155, 156, Pl. 31, figs. 5, 6.

Provedora starquistae Lochman, 1948; Alokistocaridae; middle Arrojos Formation; Proveedora Hills; 801i; USNM 115747-52; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 214, 215, Pl. 23, figs. 12, 22-28; Cooper et al., 1952, p. 156, 157, Pl. 21, figs. 12, 22-28; Lochman, 1948, p. 459, Pl. 70, figs. 7-14.

Ptarmigania hispinosa Lochman, 1952; Ptarmiganidae; middle Arrojos Formation; Proveedora Hills; 801j; USNM 115760-65; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 183-185, Pl. 24, figs. 1-9; Cooper et al., 1952, p. 133, 134, Pl. 22, figs. 1-9.

"*Ptychoparia*" sp. aff. "*P.*" *clusia* Walcott, 1917; Ptychopariidae; Arrojos Formation; Difuntos Hills; 802b; USNM 115824-27; Stewart et al., 1984, p. 18; Cooper et al., 1956, p. 188-190, Pl. 26, figs. 27-30; Cooper et al., 1952, p. 123-125, Pl. 29, figs. 27-30.

Sombrerella mexicana Lochman, 1948; Ptychopariidae; middle and upper Buelna Formation; Prieto Hill; 809a, USNM 115711-12; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 154, 155, Pl. 22, figs. 1-4; Cooper et al., 1952, p. 107, 108, Pl. 20, figs. 1-4.

Sonoraspis sp.; Ptarmiganidae; middle and upper Arrojos Formation; see *Glossopleura* sp.; Lochman regards these as *Glossopleura* sp., Stoyanow as *Sonoraspis* (see footnote by G.A. Cooper on p. 137 of Cooper et al., 1952).

Strotocephalus arrojosensis see *Amecephalus arrojosensis*.

Trilobite in cross section; base of unit 2 of the Puerto Blanco Formation; Cerro Rajón area; sample 7 of 3/23/90; field observation by M.A.S. McMenamin, March 1990; unpublished field notebook #6, p. 9.

Wanneria mexicana prima Lochman, 1952; see *Laudonia mexicana* (Lochman, 1952).

Wanneria sp.; Olenellidae; unit 4 of the Puerto Blanco Formation, Proveedora Quartzite, Buelna Formation; Proveedora Hills, Buelna Hills; sample 4 of 12/12/82; 807j; USNM 115701-02; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 145, Pl. 19, figs. 7, 8; Cooper et al., 1952, p. 99, Pl. 19, figs. 7, 8.

Wanneria walcottana buelnaensis Lochman, 1952; Olenellidae; Buelna Formation; Buelna Hills; 807b; USNM 115695-700; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 144, 145, Pl. 21, figs. 1-6; Cooper et al., 1952, p. 98, 99, Pl. 19, figs. 1-6.

Zacanthoides sp. aff. *Z. holopygus* Resser, 1939; Zacanthoidae; upper Arrojos Formation; Arrojos Hills, Proveedora Hills; 800e', 801n; USNM 115978-79, 115981-85; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 197, 198, Pl. 32, figs. 11-17; Lochman, 1953, p. 486; Cooper et al., 1952, p. 143, 144, Pl. 30, figs. 11-17.

Ostracodes

Ostracode, phosphatic shell material; unit 3 of the Puerto Blanco Formation; Cerro Rajón area; sample MM-82-49; McMenamin and McMenamin, 1990, p. 81, Fig. 4.29.

Echinoderms

Echinoderm ossicles; units 3 and 4 of the Puerto Blanco Formation, Buelna Formation; Sierra del Viejo, Cerro Clemente, Cerro Rajón area, Proveedora Hills (*Gogia?* Sprinkle, 1973), Arrojos Hills; samples MM-82-83, 2 of 12/15/82, MM-82-51c; 800b; Sprinkle, 1973, Fig. 25.

Soft-bodied fossils

Discoidal impression; Cerro Rajón area; unit 1 of La Ciénega

- Formation; sample 2 of 3/22/90; this object may be the internal sand skeleton of an actinarian resembling *Protolyella*, although an inorganic origin, such as a starved ripple or flaser bed, cannot be ruled out (McMenamin et al., 1990). Recent sectioning is consistent with the interpretation of this isolated object as a fossil.
- Arumberia?* sp.; Cerro Rajón area; unit 1? of the Clemente Formation; sample 1 of 3/22/90. Recent study (by sectioning and examination of broken rock edges) shows that this fossil, first reported by McMenamin et al. (1990), has internal structure within its enclosing rock matrix. Thus it cannot represent small gutter casts, but neither does it closely resemble any known specimen of *Arumberia*. Study of this enigmatic form is continuing.
- ?Unicellular remains and filaments*
- cf. *Eomycetopsis* Schopf, 1968; unit 2 of El Arpa Formation; Cerros El Arpa; sample MM-82-62; slide MM-82-62C (millimeters from reference $x=26.3 \times 10.4$), 1 of 3/19/90 (a new locality from the northern Cerros El Arpa, currently under study); McMenamin, 1984, p. 186, Pl. 4, fig. 2 (slide with fossil, MM-82-62C [not MM-82-62A as listed] has been relocated); Stewart et al., 1984, p. 19; McMenamin et al., 1983, p. 229, Fig. 3f (should be listed as "slide MM-82-62C" not "MM-82-62A").
- Girvanella* sp. cf. *G. sinensis* Yabe, 1912; Porostromata; middle Arrojos Formation; Proveedora Hills; 801m; USNM 115659; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 52, 53, Pl. 8, figs. 1, 2; Cooper et al., 1952, p. 25, Pl. 6, figs. 1, 2.
- Girvanella mexicana* Johnson, 1952; Porostromata; lower Buelna Formation; Buelna Hills; 807e; USNM 115658a; Stewart et al., 1984, p. 19; Cooper et al., 1956, p. 52, Pl. 8, figs. 3-5; Cooper et al., 1952, p. 24, Pl. 6, figs. 3-5.
- Radiating filaments; ?Beggiatoaceae; unit 2 of El Arpa Formation; Cerros El Arpa; sample MM-82-62; slide MM-82-62 (millimeters from reference $x=14.3 \times 28.3$); Stewart et al., 1984, p. 19; McMenamin et al., 1983, p. 230; some of these filaments are now known to be septate.
- "Algal" boundstones
- "*Collenia*"-like low domes; Cerro Rajón area; unit 4 of the Papalote Formation; sample MM-82-39; IGM 3628; Stewart et al., 1984, p. 19; McMenamin, 1984, Pl. 14, fig. 5.
- Conophyton* Maslov, 1937; upper unit, Gamuza Formation; Cerrito de la Milla, Cerros Pitiquito, Cerro Gamuza, Cerro Rajón area, Cerros El Arpa, Cerros Calaveras, Cerros de la Berruga, Sierra del Viejo, Rancho San Agustín, Cerros Aquitini; samples MM-82-33 (Rajón), MM-82-62 (Pitiquito), MM-82-60 (El Arpa), MM-82-82 (Viejo); IGM 3627; McMenamin and McMenamin, 1990, p. 12, Fig. 1.4 (IGM 3627); McMenamin, 1984, p. 33-34, Pl. 4, figs. 3 (IGM 3627), 4, 6; Stewart et al., 1984, p. 13, Fig. 8A, 8B (specimen number for Fig. 8A should be "MM-82-83" not "MM-62-33"; specimen is IGM 3627), p. 19; Cevalloz-Ferriz et al., 1982, p. 3-5, Figs. 1-3; McMenamin, 1982; Cevalloz-Ferriz, 1981; Cevalloz-Ferriz and Weber, 1980, p. 98, 99, Figs. 1, 2; Weber and Cevalloz-Ferriz, 1980, p. 106-107, Figs. 1, 3, 4; Gamper and Longoria, 1979, p. 100-102, Figs. 7, 9, 10.
- Girvanella* sp. (refers to oncolites presumed to have been formed by *Girvanella*); Buelna Formation, Arrojos Formation, Cerro Prieto Formation; Proveedora Hills, Buelna Hills, Cerro Rajón, Cerros de la Ciénega, Cerro Prieto, Cerro Clemente, Sierra del Viejo; sample MM-82-59 (Buelna Formation; Rajón); Stewart et al., 1984, p. 19,
- 22.
- Jacutophyton* Shapovalova, 1968; upper unit, Gamuza Formation; Cerrito de la Milla, Cerro Pitiquito, Cerro Gamuza, Cerro Rajón area, Cerros El Arpa, Cerros Calaveras, Cerros de la Berruga, Sierra del Viejo, Cerros Aquitini; most examples too massive to collect; Stewart et al., 1984, p. 13, 19, Fig. 8B, p. 19; McMenamin, 1984, p. 33, 34, Pl. 4, fig. 6; Cevalloz-Ferriz et al., 1982, p. 3-5, Figs. 4, 5; McMenamin, 1982; Cevalloz-Ferriz, 1981; Cevalloz-Ferriz and Werber [sic], 1980, p. 97, 102; Weber and Cevalloz-Ferriz, 1980, p. 106, 107, Figs. 1, 2, 4.
- Noncarbonate stromatolites; Puerto Blanco Formation; Awramik et al., 1978, p. 172. This occurrence has been noted by Cloud and Semikhatov (in preparation); to our knowledge, this paper has not yet been published.
- Platella* Koroljuk, 1963; upper unit, Gamuza Formation; Cerros al SW de La Ciénega, Cerros Calaveras, Cerrito de la Milla; most examples too massive to collect; McMenamin, 1984, p. 33, 34; Stewart et al., 1984, p. 19; Cevalloz-Ferriz et al., 1982, p. 3-5, Figs. 6, 8; Cevalloz-Ferriz, 1981; Cevalloz-Ferriz and Werber [sic], 1980, p. 98, 99, Figs. 1, 2; Weber and Cevalloz-Ferriz, 1980, p. 107, Figs. 3, 4.
- Thrombolites; Gamuza Formation; Cerros de la Berruga; from M.A.S. McMenamin, unpublished field notebook #4, p. 79, entry of March 15, 1982: "Some conophytons are well-preserved, but others have that 'ghost' look: columns become silty tan gray and the intercolumn sediment becomes dark gray, forming a mottled 'airbrush' reticulate pattern on the surface of the dolostone. Laminations are obliterated...."
- Trace fossils*
- Astropolithon?* sp.; unit 3 of the Puerto Blanco Formation; Cerro Rajón area; uncollected float block, same horizon as sample 7 of 12/17/82; McMenamin, 1984, p. 108, 109, Pl. 7, figs. 3, 4.
- Bergaueria radiata* Alpert, 1973; upper unit 4 of the Puerto Blanco Formation; Cerro Rajón area; sample MM-82-54; IGM 3638; McMenamin, 1984, p. 92, Pl. 9, fig. 3; Stewart et al., 1984, p. 19 (listed as *Bergaueria*).
- Cruziana semiplicata* Crimes, 1968; unit 3 of the Puerto Blanco Formation; Cerro Rajón area; sample 7 of 12/17/82; IGM 3622; McMenamin and McMenamin, 1990, p. 40, Fig. 3.7; McMenamin, 1984, p. 103, 104, Pl. 6, fig. 5.
- Cruziana* sp.; units 3 and 4 of the Puerto Blanco Formation, Buelna Formation, Arrojos Formation; Cerro Rajón area; Stewart et al., 1984, p. 19 (listed as *Cruziana*).
- Dactyloidites asteroides?* (Fitch, 1850); unit 3 of the Puerto Blanco Formation; Cerro Rajón area; uncollected float block, same horizon as sample 7 of 12/17/82; McMenamin and McMenamin, 1990, p. 42, Fig. 3.9; McMenamin, 1984, p. 109, 110, Pl. 7, figs. 1, 2.
- Endolithic borings (casts) on degraded echinoderm ossicle; Buelna Formation; Angustra Pass area, Sierra del Viejo; sample MM-82-83; McMenamin and McMenamin, 1990, p. 145, Fig. 8.6.
- Fucusopsis* sp.; unit 3 of the Puerto Blanco Formation; Cerro Rajón area; sample 6.75 of 12/19/82; IGM 3641; identified by A. Seilacher.
- Indeterminate curving impressions; unit 2 of the Puerto Blanco Formation; Cerro Clemente and Cerro Rajón area; samples 1 of 12/14/82 and 4.5 of 12/17/82; IGM 3623-24; McMenamin, 1984, p. 105-107, Pl. 6, figs. 6-8. These specimens, which consist of concentric, evenly spaced fine grooves, may actually be poorly preserved body fossil (?brachiopod) material.

Monomorphichnus sp.; unit 3 of the Puerto Blanco Formation; Cerro Rajón area; sample 7 of 12/17/82; IGM 3621; McMenamin, 1984, p. 104, 105, Pl. 6, fig. 4.

Palaeophycus reticulatus (Alpert, 1975); unit 3 of the Puerto Blanco Formation; Cerro Rajón area; sample 7 of 12/17/82; IGM 3636; McMenamin, 1987b, p. 99, upper figure; McMenamin, 1984, p. 93, 94, Pl. 9, fig. 1.

Palaeophycus sp.; Puerto Blanco Formation, Buelna Formation, Arrojos Formation; Cerro Rajón area; Stewart et al., 1984, p. 19.

Palaeophycus sp. cf. *P. alternatus* Pemberton and Frey, 1982; unit 3 of the Puerto Blanco Formation; Cerro Rajón area; sample 7 of 12/17/82; IGM 3639; McMenamin, 1984, p. 93, Pl. 9, figs. 4, 5.

Palaeophycus tubularis Hall, 1847; unit 1 of La Ciénega Formation, Puerto Blanco Formation; samples 6.75 of 12/19/82 and MM-82-53; IGM 3640-41; McMenamin, 1984, p. 94, 95, Pl. 9, figs. 6, 7.

Planolites montanus Richter, 1937; Cerro Rajón area; unit 1 of La Ciénega Formation; sample 1 of 3/23/90. This is the specimen referred to as *Gordia* in McMenamin et al. (1990).

Rusophycus sp.; unit 3 of La Ciénega Formation; Cerro Rajón area; sample MM-82-49a; IGM 3619; McMenamin, 1984, p. 107, 108, Pl. 6, figs. 1, 2; Stewart et al, 1984, p. 19. This trace is interpreted here as a trilobitoid ichnofossil, but the form is enigmatic and subject to other interpretations.

Scolicia fossulata (Fenton and Fenton, 1937); unit 3 of the Puerto Blanco Formation; Cerro Rajón area; sample 7 of 12/17/82; IGM 3634; McMenamin, 1984, p. 96, Pl. 8, fig. 5.

Scolicia sp.; units 2 and 3 of the Puerto Blanco Formation; Cerro Rajón area; sample 7 of 12/17/82; IGM 3625; McMenamin and McMenamin, 1990, p. 40, Fig. 3.6; McMenamin, 1987b, p. 99, lower figure; McMenamin, 1984, p. 96, 97, Pl. 7, figs. 5, 6; Stewart et al., 1984, p. 19.

Scolicia sp. A; unit 2 of the Puerto Blanco Formation; Cerro Rajón area; sample 6 of 12/17/82; IGM 3620; McMenamin, 1984, p. 97, 98, Pl. 6, fig. 3.

Scolicia sp. B; unit 1 of the Puerto Blanco Formation; Cerro Rajón area; sample 1 of 12/19/82; McMenamin, 1984, p. 98, 99, Pl. 8, fig. 4.

Scolicia sp. C; unit 2 of the Puerto Blanco Formation; Cerro Rajón area; samples MM-82-47 and 4.5 of 12/17/82; IGM 3635, 3637; McMenamin, 1984, p. 99, Pl. 8, fig. 6, Pl. 9, fig. 2.

Shell boring on shell fragment (possibly an inarticulate brachiopod); unit 2 of the Puerto Blanco Formation; Cerro Rajón area; sample 5.5 of 12/17/82; IGM 3614[38]; McMenamin, 1986, p. 179, Figs. 1, 2.

Skolithos bulbosus Alpert, 1975; unit 2 of the Puerto Blanco Formation; Cerro Rajón area; sample 7 of 12/19/82; IGM 3632; McMenamin, 1984, p. 100-102, Pl. 8, figs. 1, 2.

Skolithos linearis Haldeman, 1840; basal Proveedora Quartzite, unit 4 of the Puerto Blanco Formation; Cerro Clemente; sample 3 of 12/15/82; IGM 3633; McMenamin and McMenamin, 1990, p. 38, Fig. 3.5 (figure is upside down); McMenamin, 1984, p. 102, 103, Pl. 8, fig. 3; same as *Skolithos* sp. of Stewart et al., 1984, p. 19.

New Jersey fossils

Archeocyathans

Archaeocyathus sp. (*Pycnoidocyathus* sp.); Flindersicyathidae, Leithsville Formation; Franklin, NJ; 1 of 10/19/89; Palmer and Rozanov, 1976, p. 774, Fig. 1B.

Dictyocyathus sp.; Dictyocyathidae; Leithsville Formation; Franklin, NJ; Palmer and Rozanov, 1976, p. 774.

Protopharetra sp.; Protopharetridae; Leithsville Formation; Franklin, NJ; 1 of 10/19/89; Palmer and Rozanov, 1976, p. 774, Fig. 1A.

Representative of the Superfamily Ajacicyathacea; Leithsville Formation; Franklin, NJ; 1 of 10/19/89; NYSM 16133; Palmer and Rozanov, 1976. The number of pores per intersept on the inner wall is not determinable; if this specimen were well-enough preserved, it could be placed in one of the two families, Ajacicyathidae or Robustocyathidae, of the Superfamily Ajacicyathacea. See Plate 1.2, this report.

Brachiopods

Brachiopod indet.; Leithsville Formation; Franklin, NJ; 1 of 10/19/89; NYSM 16134.

Hyoliths

Hyolithid or orthothecid; Leithsville Formation; Franklin, NJ; 1 of 10/19/89; NYSM 16134; transverse section of shell found in petrographic thin section. See Plate 1.4, this report.

Trilobites

Trilobite "shepherd's crooks" in petrographic thin section; NYSM 16134; Leithsville Formation; Franklin, NJ; 1 of 10/19/89.

Acknowledgments

We thank S.R. Roof for assistance with thin sectioning, S.R. Dunn and M.M. Godchaux for discussion of the volcanics in the Puerto Blanco Formation, G.M. Narbonne and A. Seilacher for identification of trace fossils, W.H. Fritz for discussion of trilobites, S.W.F. Grant for discussion of the cloudinids, and P.W. Signor and S.M. Rowland for reviews. This research was supported by NSF Grant EAR 8857995, which supplied \$1,500 toward publication of this report.

Repository

Fossil repositories are abbreviated as follows: IGM (Institute of Geology Museum, Mexico City), MNHN (Museum of Natural History, Paris), NYSM (New York State Museum Paleontology Collection, Albany) and USNM (United States National Museum, Washington, D.C.).

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Note added in proof

Mickwitzia lochmana and *multipuncta* have been described from unit 3 (Provedora Hills) and Unit 2 (Cerro Rajon), respectively, of the Puerto Blanco Formation (M.A.S. McMenamin, 1992, "Two new species of the Cambrian genus *Mickwitzia*," *Journal of Paleontology* 66:173-192. [In the letter report, the scale bar value in the caption of Fig. 1.3 should be corrected to read 2 mm.]

W. Fritz (1992, "Walcott's Lower Cambrian olenellid trilobite collection 61K, Mount Robson area, Canadian Rocky Mountains," *Geological Survey of Canada Bulletin* 432:21) recommended placing *Nevadia ovalis* McMenamin, 1987 [misspelled "*ovatis*" in Fritz, 1992] in the genus *Nevadella*.

Debrenne and Zhuravlev (1992, "Irregular archaeocyaths," CNRS Editions, Paris, 212 p.) revised *Palmericyathellus undatus* Debrenne, 1989, to *Spirocyathella spinosa* (Debrenne). Debrenne and Zhuravlev (1992) illustrated the Mexican archaeocyathans *S. spinosa* (Debrenne)

(their Pl. 17, fig. 3), *Stevocyathus elictus* Debrenne, 1989 (their Pl. 10, fig. 5), and *Markocyathus clementensis* Debrenne, 1989 (their Pl. 13, figs. 1, 3).

Correlation of facies divisions in the uppermost Ludlowville Formation (Givetian) across western and central New York State

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Abstract

The Spafford and Jaycox Members, the youngest units of the Ludlowville Formation within the Middle Devonian Hamilton Group, are richly fossiliferous and geographically widespread. They record deposition in subtidal muddy shelf settings along the northern margin of the Appalachian Basin. In the type area near Skaneateles Lake, the bottom two thirds of the 7-8 m Spafford Member is an interval of shell-rich shale; the upper third is more sparsely fossiliferous silty mudstone and siltstone. Although the Member has not been recognized west of Owasco Lake, new correlation demonstrates its gradation into an interval of very sparsely fossiliferous mudstones delimited at the base by a condensed shell-rich concretionary bed (Limerick Road Bed). As thus defined, the Spafford Member is now traced westward to the Genesee Valley area, where it is truncated beneath the Jaycox Member. Mudstones of the Spafford Member, though sparsely fossiliferous, yield abundant remains of a problematic soft-bodied organism at one level, which suggests that distal mud tempestite events were particularly important in this facies. The typical western facies of the Jaycox Member consists of 0.2 to 5.0 m of calcareous mudstone with widespread shell beds. The Jaycox Member is marked at its base by a 20-50 cm-thick calcareous mudstone to packstone, the Hill's Gulch Bed. Thick (>10 m) mudstone deposits of the Jaycox Member accumulated differentially in a subsiding trough ("Romulus Sag") centered in the Seneca-Cayuga Valley region, and thin (0-10 m) deposits accumulated east and west of this trough. Lithologic divisions of the Jaycox Member thin away from the trough because of the combined effects of submarine erosion and sedimentary condensation; the mudstones grade westward into shell- and coral-rich siltstones and limestones. Post-Jaycox erosion, associated with a major regression that preceded deposition of the overlying Moscow Formation, has removed variable amounts of the Jaycox Member on both southeastern and western ramp areas; the least erosion is evident near the axis of the Romulus Sag.

Detailed mapping of the Hill's Gulch Bed of the lower Jaycox Member shows that this shell-rich unit records shoaling events west of the sag, and can be correlated with a shell-rich siltstone and sandstone unit (Owasco Siltstone). The Owasco Siltstone overlies the uppermost Spafford Member in the shelf tract east of the trough (or Green's Landing Coral Bed), although post-Jaycox erosion has removed part of the evidence. The Spafford-Jaycox interval, which records the lower part of a widespread regressive event (Tichenor regression-transgression cycle), contains evidence of at least four cyclic facies alternations

caused by minor regressive-transgressive events superimposed on the larger regression trend.

Introduction

An important facet of stratigraphy is the correlation of thin, widespread event beds across major facies tracts and between regions of pronounced thickening or thinning of coeval sedimentary deposits. Because event beds are often isochronous or nearly so, successful matching of these units across facies strike and across sedimentary basins allows workers to subdivide facies wedges and belts into time-constrained depositional packages that can more easily be studied by process sedimentology and paleoecologic methods (see Heckel, 1973; Baird and Brett, 1981; Baird et al., 1988). Such correlations can be cross-checked through biostratigraphic sampling. However, event-bed correlation should yield a far more finely resolved chronostratigraphy than traditional biostratigraphy. Biotic zones usually encompass longer duration sedimentary intervals that can be more finely subdivided by successions of distinctive storm beds, concretion layers, ash beds, diastems, and other taphonomic features. In addition, the observed local vertical zonal range is always less than the actual evolutionary "lifetime" of the given taxon.

Stratigraphic advances during the past fifteen years have centered on the recognition that the sedimentary record is largely composed of isochronous sedimentary cycles and sequences of varying scales. These cycles are products of global changes in climate, sea level, and tectonic regimes (see Dennison and Head, 1975; Van Wagoner et al., 1988; Baum and Vail, 1988). Stratigraphers must recognize the presence and extent of sedimentary cycles within a basin and be able to separate allocyclic controls from the overprinted effects of intrabasinal tectonic history, as well as recognize the dynamic interaction between changes in sediment supply and sediment accommodation space (see Klein and Willard, 1989). A first step in determining whether a marker bed or cyclic unit may be either the product of local autocyclic factors or allocyclic events is to attempt correlation within the various facies tracts of a sedimentary basin. The lithologic expression of a marker bed should vary with the depositional setting, but these varying lithologies should correlate if they are the product of a widespread event. Once these correlations have been made around or across a basin, they must be correlated into other basins in order to confirm a eustatic character (see Heckel, 1986, for interbasinal correlation of Pennsylvanian cyclothems).

This report examines several regionally extensive event-beds within subtidal shelf and basin margin facies in a Middle Devonian New York foreland basin sequence. The Spafford and Jaycox Members, the upper two members of the Ludlowville Formation (Hamilton Group), are divisible into thin, but geographically widespread, stratigraphic units. Refined correlation is based on the use of concretionary carbonate beds, prominent coral beds, "barren" shale intervals, diastems, and a unit rich in problematical, discoidal, soft-bodied organisms. These units are described in terms of their regional facies character and probable depositional setting, particularly with regard to their proximity to sources of terrigenous sediment deposited on the marine shelf and in a subsiding trough ("Romulus Sag"; see Figure 1) that bisected the shelf. The lowest unit of the Spafford Member is a brachiopod-coral-rich condensed bed (Limerick Road Bed) that, locally in the Finger Lakes region, contains reworked and encrusted concretions; this unit appears to amalgamate with other shell beds to the east. Key condensed marker horizons permit unambiguous correlations of the upper Ludlowville Formation across major facies changes in the Romulus Sag.

An important limestone unit (Hill's Gulch Bed) at the base of the Jaycox Member west of the Romulus Sag correlates with a siltstone/fine-grained sandstone (Owasco Siltstone) east of the trough. An intervening thicker wedge of siliciclastic mudstone is a characteristic transitional facies in the trough depocenter. This facies arrangement indicates that the Hill's Gulch-Owasco interval marks a widespread regression event that may be recorded wherever coeval Devonian deposits are preserved in the Appalachian Basin. Such correlations cannot be confidently made with the marker beds of the upper Jaycox Member; the evidence has been removed by post-Ludlowville erosion.

In addition, the Romulus Sag was an active subsiding feature during Jaycox deposition that affected deposition of all subdivisions of the Jaycox Member, as well as underlying and overlying units. Troughward thickening of Jaycox beds, with attendant downslope facies changes, is closely associated with downslope loss, or near-loss, of discontinuities. In addition, shelfward facies transitions to thin calcareous units (in the west) and thin sandstone units (in the east) preceded erosional beveling of the condensed facies in the shallower settings.

The patterns of event-bed sequences, as well as the facies and thickness trends of these divisions, are used to show that at least four regressive subcycles appear to be superimposed on a larger regressive trend within the Jaycox Member. The post-Jaycox discontinuity beneath the high energy facies (Tichenor Limestone) of the lowermost Moscow Formation illustrates the relationship of the Jaycox (and Tichenor) facies to the larger (fourth-order?) Tichenor regressive cycle, of which the Jaycox is a part. Finally, the facies and thickness trends within the Jaycox Member mirror those observed in beds both below and above the Tichenor. Event beds provide evidence for the lateral, westward migration of the depocenter of the Romulus Sag, apparently as a result of basin flexing over several million years.

Geologic setting

Paleogeography

The study area in western and central New York is situated at the northern end of the Appalachian foreland basin and at the northern outcrop limit of Middle Devonian (Givetian) marine deposits. In the Middle Devonian, this area was probably located in the subtropical or warm temperature belt at about 30° south latitude (Witzke and Heckel, 1988), but it may have been farther north within the southern tropics

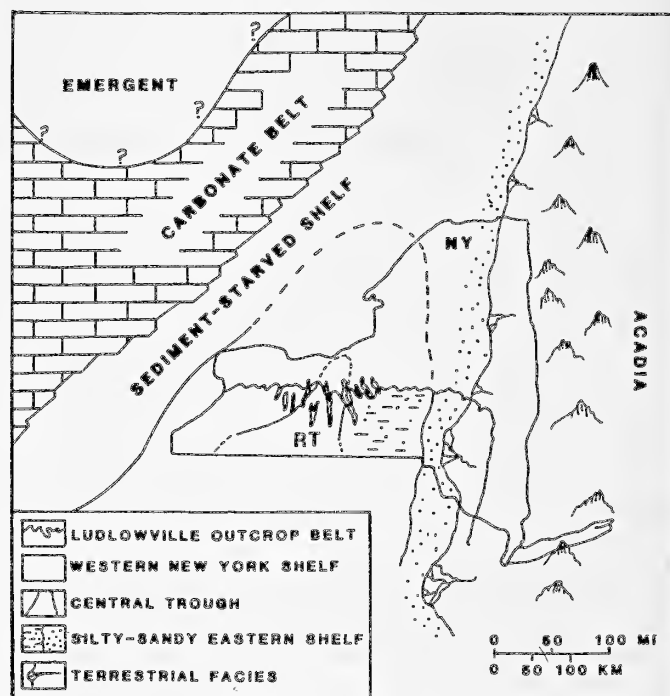


Figure 1. Generalized depositional setting and paleogeography of New York State and surrounding areas during Middle Devonian (Givetian) time. Modified from Mayer (1989).

(see Van der Voo, 1988). A broad subtidal shelf in western and central New York was bounded by the active Acadian orogenic belt to the east and southeast, and by a broad region of shallower restricted marine waters and subaerial craton to the northwest and north (Figure 1). To the south and southwest was a region of deeper subtidal water closer to the actively subsiding foreland basin. Erosion of the rising Acadian Mountains released large quantities of siliciclastic sediment into the basin, which resulted in local delta progradation to produce the Catskill Delta complex (Figure 1). By Givetian time, the easternmost parts of the foreland basin had been filled in and the region of terrigenous sediment influx extended as far west as Ohio and southern Ontario (see Woodrow, 1985; Etensohn, 1987). Major eastward thickening and coarsening of Middle and Upper Devonian terrigenous deposits, and the westward advance of terrestrial facies across New York State during this period, provide evidence for this influx.

During deposition of the Jaycox Member, most of the study area was a shallow subtidal (infralittoral) shelf that was variably influenced by siliciclastic mud influx (Baird, 1979; Baird and Brett, 1981; Mayer, 1989). However, a northeast-southwest-trending region of slightly deeper water and active subsidence, the Romulus Sag, bisected the shelf in the present-day central Finger Lakes region; during Jaycox deposition, the trough axis was located in the region between Seneca and Cayuga Lakes (Baird and Brett, 1981; Mayer, 1989; Figure 1). West of this trough, only fine siliciclastic sediment accumulated in association with biogenic carbonate, but east of the trough the shelf region received variable amounts of siliciclastic silt and fine sand with a reduced biogenic carbonate component. The deeper trough region was a depocenter for the accumulation of siliciclastic mud with only minor fractions of silt, sand, and fossil fragments. West of the trough, where siliciclastic sediment influx was reduced, optimal bottom conditions often support-

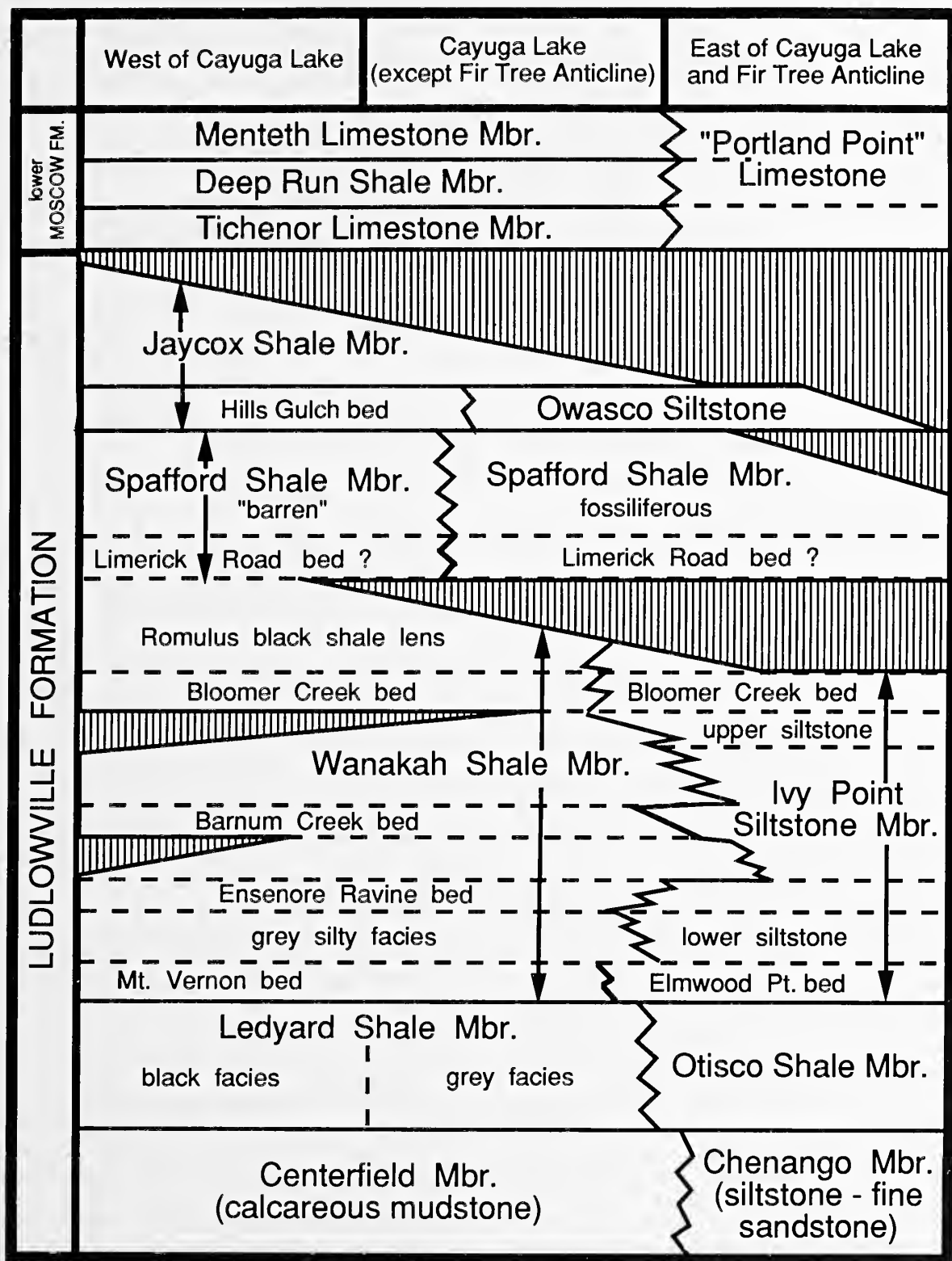


Figure 2. Schematic chronostratigraphy of the Ludlowville Formation in west-central New York State showing correlations discussed herein. Modified from Brett et al. (1986).

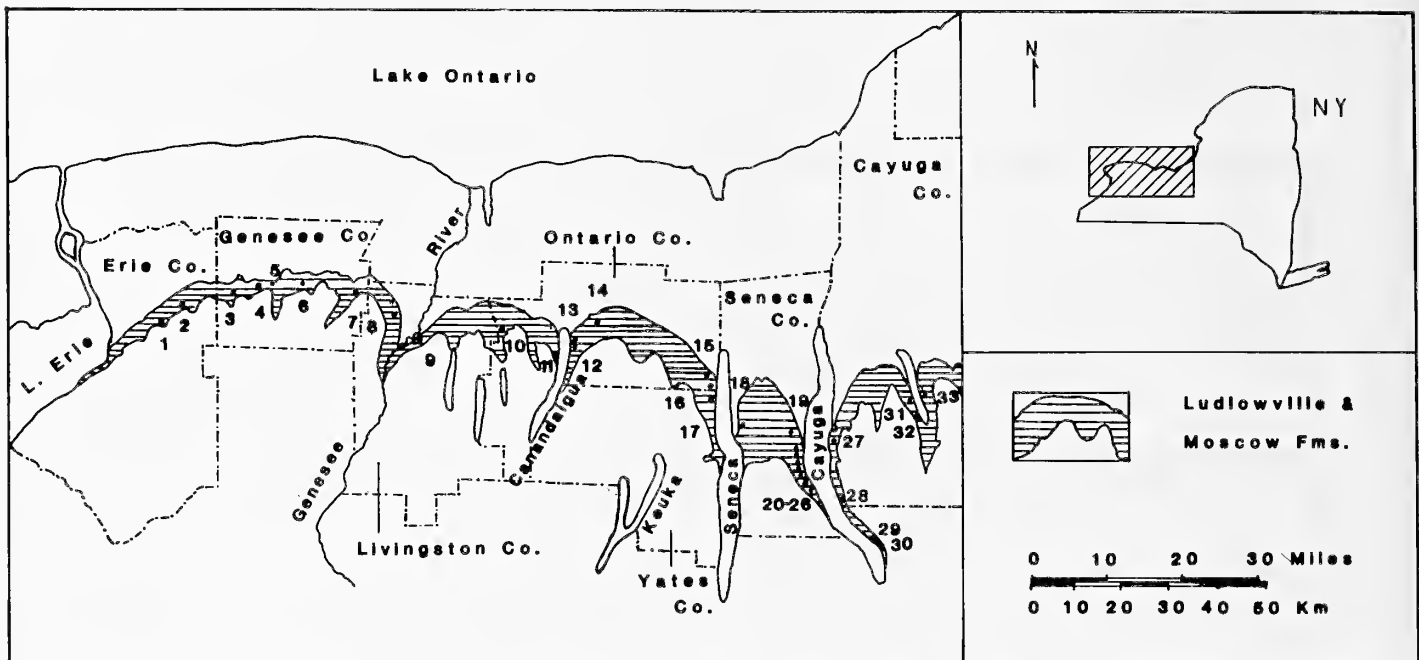


Figure 3. Outcrop belt of Ludlowville and Moscow Formations showing key sections discussed in text. Numbered sections are listed in the locality register (Appendix I). Modified from Baird (1979).

ed diverse benthic organisms, particularly large rugose and tabulate corals, brachiopods, bryozoans, and pelmatozoans.

Stratigraphy

The Spafford and Jaycox Members are Middle Devonian units (lower *Polygnathus varcus* conodont Zone of the middle Givetian Stage; see Rickard, 1975). These Members are the uppermost divisions of the Ludlowville Formation, the third of four formations that constitute the Middle Devonian Hamilton Group in New York State (Figure 2). In western New York State, the upper half of the Hamilton Group, including the Ludlowville Formation and the overlying Moscow Formation, consists mainly of fossiliferous grey mudstone with subordinate dark grey mudstone; fossiliferous concretionary, fine-grained carbonate units; and thin calcarenitic limestone beds.

The Ludlowville Formation of western New York has been subdivided into four members: the Centerfield Limestone (4-14 m), Ledyard Shale (10-30 m), Wanakah Member (12-21 m), and Jaycox Member (0.25-18.0 m) (Cooper, 1930; Baird, 1979). In central New York, the Ludlowville Formation consists mainly of variably silty mudstones with lesser proportions of fossiliferous siltstone and sandstone. Smith (1935) subdivided the Ludlowville Formation of the Skaneateles-Owasco Lake region above the Centerfield Member (which Smith included in the Skaneateles Formation) into four units (in ascending order): Otisco Shale (50 m), Ivy Point Siltstone (20 m), Spafford Shale (8 m), and Owasco Siltstone (0.2-2.5 m) (Figure 2). Until recently, it has remained unclear how these units correlate with western Ludlowville units. A major thrust of recent studies by the authors of this report has been to establish precise correlations between Smith's (1935) units and those of western New York.

The Otisco Shale has been unambiguously correlated with the black Ledyard Shale, and the Ivy Point Siltstone equated with parts of the Wanakah Member (Brett et al., 1986); however, the precise relationship

of the Spafford Member and Owasco Siltstone to the post-Wanakah Ludlowville Formation has remained somewhat problematical. Near Skaneateles Lake, the Spafford Member consists of about 4-5 m of brachiopod-bivalve-rich shale that grades upward into sparsely fossiliferous silty mudstone and siltstone. The Spafford Member can be traced eastward at least to the Chenango Valley with little facies change. However, it was not recognized west of Owasco Lake.

Recently, Mayer et al. (1990) recognized that Smith's (1935) Spafford Member extended westward into the Cayuga and Seneca Lake region as a 7-8 m interval of sparsely fossiliferous siliciclastic mudstone that contains undescribed problematical fossils. This interval is recognized farther west as a thin tongue of shale, formerly assigned to the Wanakah Member, at and slightly west of the Jaycox type section. It is delimited at its base by a shell-rich bed (Limerick Road Bed) and at the top by the Hill's Gulch Bed.

The Jaycox Member, which reaches a maximum thickness of approximately 20-25 m near Romulus, Seneca County, extends from the vicinity of Elma, Erie County, eastward to the meridian of Syracuse. West of Elma and east of Syracuse, the Jaycox Member is largely to completely absent as a result of erosional beveling. The Jaycox Member is underlain by fossiliferous grey siliciclastic mudstone deposits of the Wanakah Member from Erie County eastward to East Bethany. From Genesee County eastward, grey, variably silty and fossiliferous siliciclastic mudstones, herein assigned to the Spafford Member, are interposed between the Wanakah Member and the basal layer (Hill's Gulch Bed) of the Jaycox Member (Mayer, 1989). The Jaycox Member is disconformably overlain by the Tichenor Limestone, the basal division of the overlying Moscow Formation, throughout the study area.

The Jaycox Member was proposed by Baird (1979), who recognized that this interval of thin concretionary limestones and profusely fossiliferous calcareous mudstone is distinct from the pelmatozoan grainstone-packstone deposit in which it had been formerly included (see Cooper,

1930). The Jaycox Member differs lithologically from the Tichenor Limestone and is also separated from it by a regional disconformity. Baird (1979) placed the base of the Jaycox Member at the base of a regionally widespread concretionary limestone bed that was later designated the Hill's Gulch Bed of the Jaycox Member by Kloc (1983). Thus at its designated type section on Jaycox Run in Livingston County (Loc. 9; numbered sections are listed in Appendix I), the Jaycox Member was originally defined by Baird (1979) to consist of the basal Hill's Gulch Bed and an overlying undivided calcareous mudstone sequence that contain several unnamed, profusely fossiliferous beds. Baird (1979) traced fossiliferous Jaycox beds into the Seneca Lake Valley, where they were observed to grade into sparsely fossiliferous mudstone deposits of the King Ferry Member, a poorly defined stratigraphic unit not recognized herein. Subsequent work by Mayer (1989) resulted in a reassignment of additional beds that were formerly placed in the Wanakah Member, and a detailed subdivision of beds within the Jaycox Member. In addition, Mayer et al. (1990) extended several Jaycox subdivisions eastward across the central Finger Lakes region into the Owasco Lake-Skaneateles Lake region southwest of Syracuse, thus replacing part of the earlier King Ferry designation. The above correlations of Mayer (1989) and Mayer et al. (1990) form the basis of the detailed descriptions presented herein.

Localities

Strata of the Jaycox Member are accessible at more than fifty localities along the east-west outcrop belt of the Ludlowville Formation, particularly in the Finger Lakes region where numerous streams expose the southward-dipping beds of the Hamilton Group (Figure 3). Thirty-four of these sections were studied in detail; numbered sections discussed herein are listed in Appendix I.

Stratigraphy and regional character of Spafford and Jaycox Members: Erie County-Seneca Lake region

In western New York from Erie County to Seneca County (Figure 3), the Spafford-Jaycox interval is an eastward-thickening wedge (0.2 to 18 m) of medium grey calcareous mudstone with thin shell-coral-rich condensed marker beds (Figure 4). The members and their subdivisions are correlated on the basis of these key beds. Most notable of these horizons, in ascending order, are the Limerick Road Bed (base of Spafford Member), Hill's Gulch Bed (base of Jaycox Member), and Tichenor Limestone (base of overlying Moscow Formation). These units are described in detail in the following sections.

Spafford Member

Limerick Road Bed.—The lowest unit of the Spafford Member in western New York is an 18 to 157 cm-thick layer of calcareous to somewhat silty grey siliciclastic mudstone rich in fossils, most notably molluscan debris, the tabulate coral *Pleurodictyum*, and the spiriferid brachiopods *Mediospirifer* and *Athyris*. This unit, herein designated the Limerick Road Bed for an exposure on Browns Creek (Loc. 8) upstream from the Limerick Road overpass in the town of York, Livingston County, is easily distinguished from medium grey to dark grey shales of the underlying Wanakah Member (see Figure 5). A distinctive diminutive brachiopod fauna is characteristic of the upper Wanakah beds, particularly between Erie County and Cayuga Lake.

Thus the robust fauna of the Limerick Road Bed forms an easily recognizable marker for the base of the overlying Spafford sequence.

The Limerick Road Bed is traceable from the vicinity of Bethany Center (Loc. 6) in Genesee County eastward into the Cayuga Valley (Figure 7). It is absent west of Bethany Center because of westward erosional overstep (truncation) by a diastem beneath the overlying Hill's Gulch Bed (discussed below). The Limerick Road Bed becomes unrecognizable southeast of Mack Creek (Loc. 20) in the Cayuga Valley because of complex and rapid facies changes within the upper Ludlowville section in this area. As discussed below, this unit has a basal erosional (diastemic) contact with the underlying Wanakah Member between Seneca Lake and Cayuga Lake. The most diverse fauna, and generally the most calcareous mudstone lithology, are observed in the westernmost sections. Although the base of this unit is sharp in most places and commonly characterized by a reentrant above the Wanakah Member, the upper boundary is gradational into an overlying sequence of grey mudstone that is characteristically poor in fossils.

"Barren" mudstones of Spafford Member in western New York.—Between the Limerick Road Bed and the Hill's Gulch Bed is an unnamed interval of very sparsely fossiliferous, grey siliciclastic mudstone (Figures 4-6). This unit is traceable from Hill's Gulch (Loc. 7) in Genesee County eastward into the central Finger Lakes region. It thickens eastward from only 20 cm west of the Genesee Valley (Figure 5) to as much as 2.0 m in creeks west of Seneca Lake (Figure 6; Locs. 15-17). Westward overstep of this mudstone by an erosion surface at the base of the overlying Hill's Gulch Bed results in complete beveling of the barren mudstone interval at the Bethany Center roadcut (Loc. 6). This erosional history included removal of the underlying Limerick Road Bed west of Bethany Center.

The "barren shale" facies of the Spafford Member actually contains fossils, but they are very uncommon. Blocky, grey siliciclastic mudstones in this interval yield the brachiopods *Devonochonetes coronatus*, *Tropidoleptus carinatus*, and *Mucrospirifer mucronatus*; the bivalves *Pterinopecten* sp. and *Modiomorpha subalata*; and the trilobite *Phacops rana*. Somewhat less common are patchy occurrences of the tabulates *Favosites* and *Thamnoptychia*, the brachiopod *Mediospirifer audaculus*, the gastropod *Platyceras* sp., and pelmatozoan ossicles.

Jaycox Member

Jaycox Member type section.—At Jaycox Run (Loc. 9), 3.6 m of the Jaycox Member are observed between the underlying thin tongue of the Spafford Member and the sub-Tichenor (sub-Moscow) disconformity at its top (Figure 4). The type section, as redefined by Mayer (1989) and herein, includes 0.77 m of Spafford Member-equivalent siliciclastic mudstone in the section below the Hill's Gulch Bed. This mudstone was earlier referred to the Wanakah Member by Baird (1979). This interval includes the basal Limerick Road Bed and overlying barren mudstone. Jaycox Member subdivisions at the type section include the following (in ascending order): (1) the Hill's Gulch Bed (basal Jaycox division of Baird, 1979); (2) unnamed mudstone interval; (3) *Tropidoleptus-Longispina* interval; (4) Green's Landing Coral Bed; (5) Demosponge-*Megastrophia* bed; (6) middle Jaycox barren mudstone interval; (7) Cottage City Coral Beds; and (8) upper Jaycox barren siliciclastic mudstone interval (see Figure 4).

West of this type section, the Jaycox Member becomes thinner as a result of stratigraphic condensation and erosional beveling below the Hill's Gulch Bed and Tichenor Limestone, and there is a westward change to a higher energy, bioclast-rich facies at all levels. East of the

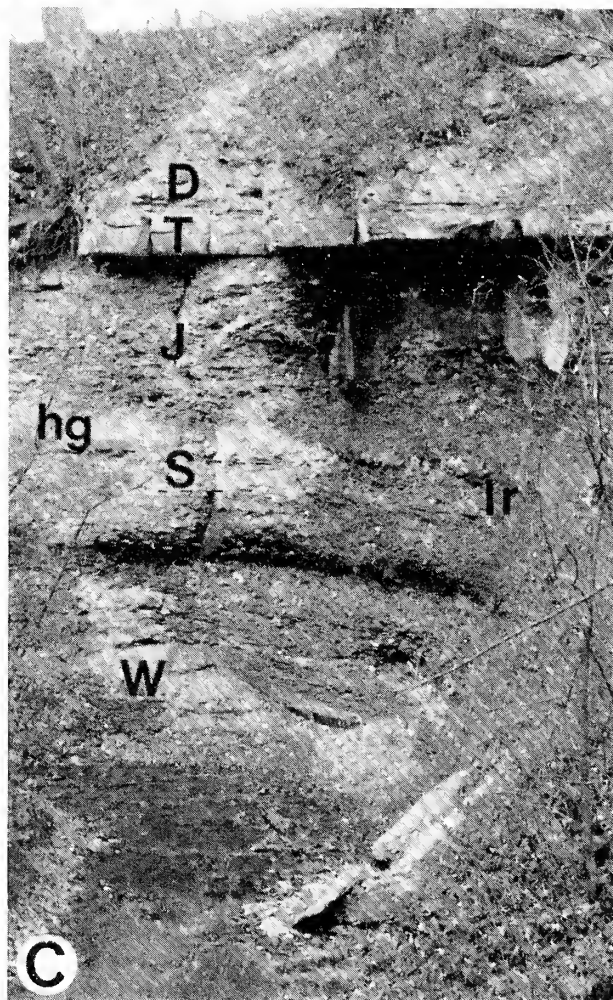
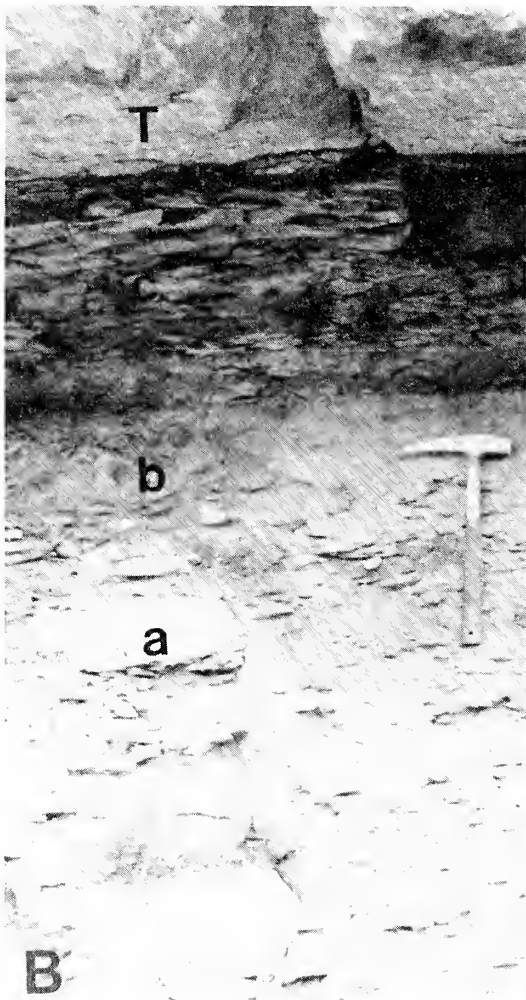


Figure 4. Jaycox Member type section (Loc. 9) along south tributary of Jaycox Creek north of Geneseo, Livingston County, New York. A, Waterfall over Tichenor Limestone (T); note sharp contact of Tichenor Limestone on upper Jaycox Member (J) and upward gradation into Deep Run Member mudstone (D). Waterfall is approximately 2.0 m high. B, Closeup of disconformable contact of Tichenor Limestone (T) on Jaycox Member; units in Jaycox include (a) middle "barren" shale interval; (b) Cottage City Coral Beds (note rugose corals); (c) unfossiliferous Benton Run Mudstone. C, View of bank downstream (west) of Tichenor waterfall (Figure 4A) showing complete Jaycox Member and synjacent units. Symbols: W=Wanakah Member; S=Spafford Member; LR=Limerick Road Bed; J=Jaycox Member; HG=Hill's Gulch Bed; T=Tichenor Limestone; D=Deep Run Member.

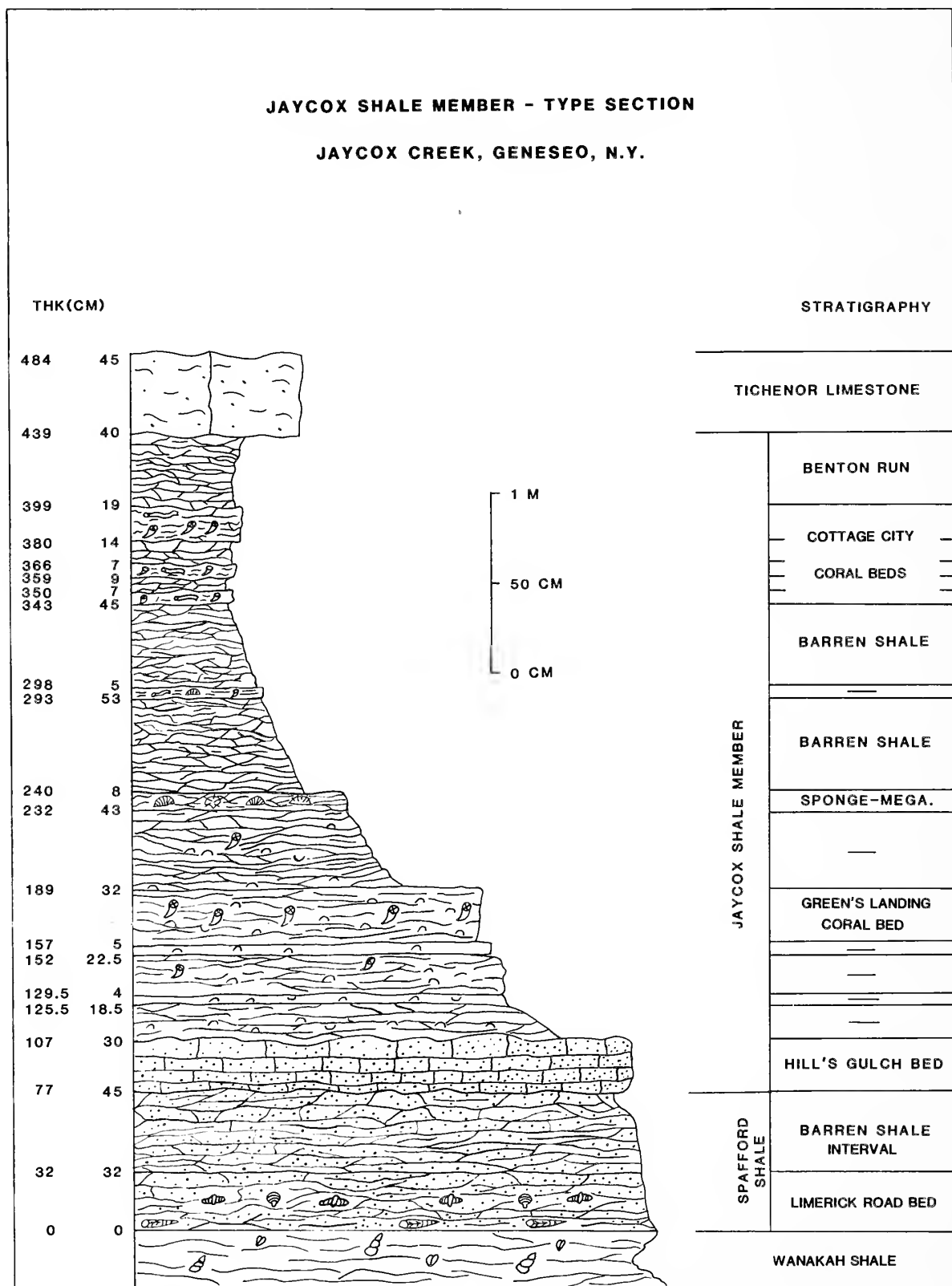


Figure 5. Stratigraphy of Jaycox Member on Jaycox Creek showing detailed units of Spafford and Jaycox Members.

type section, the Jaycox Member thickens greatly, and all of its lithologic subdivisions become more argillaceous and less fossiliferous (Figure 5). Moreover, additional Jaycox strata appear progressively eastward beneath the sub-Tichenor disconformity, and the upper Jaycox barren shale unit becomes the thickest subdivision at Seneca Lake (see Figures 5, 6).

Hill's Gulch Bed.—An erosionally resistant concretionary limestone bed (or calcareous siltstone layer), designated the "Hill's Gulch Bed" by Kloc (1983) for exposures on Hill's Gulch ravine (Loc. 7), occurs in all Jaycox sections between Cazenovia Creek (Loc. 1) in Erie County and Sampson State Park (Loc. 18) in Seneca County (Figures 3, 5, and 6). The base of this unit was designated as the base of the Jaycox Member by Baird (1979). The Hill's Gulch Bed varies irregularly in

thickness across western and central New York from 6 to 30 cm and changes eastward from a shell-coral-rich, pelmatozoan packstone west of Hill's Gulch (Figure 7) to a sparsely fossiliferous calcareous siltstone in Seneca County. At most sections between Hill's Gulch and Seneca County, it is a slightly silty, calcareous mudstone with gradational upper and lower boundaries. However, west of the Genesee Valley this unit becomes distinctly calcarenitic and has an erosional base. The base of the Hill's Gulch Bed is locally sharp and undulatory with hypichnial *Rusophycus*–*Cruziana*-type trace fossils that show abrasional enlargement by storm events; these prod-like features sometimes resemble the "tubular tempestites" of Wanless (1986). As noted above, this discontinuity first oversteps the "barren" shale interval and then the Limerick Road Bed (Spafford Member) to the west (Figure 6). Between Bowen

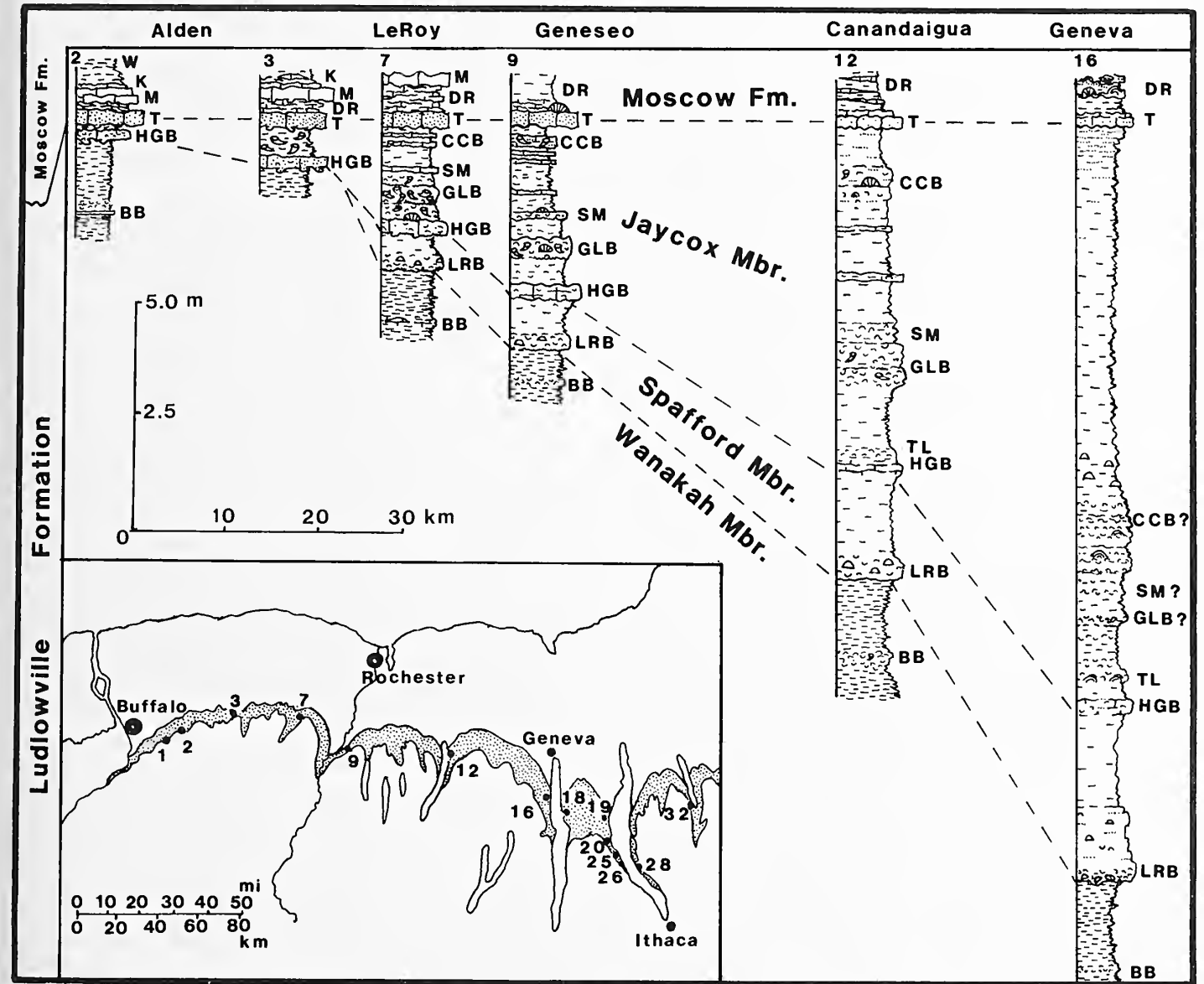


Figure 6. Correlation of Spafford and Jaycox Members and synjacent units across western New York from Erie County to Seneca Lake. Units include BB=Bloomer Creek Bed; LRB=Limerick Road Bed; HGB=Hill's Gulch Bed; TL=*Tropidoleptus*–*Longispina* mudstone interval; GLB=Green's Landing Coral Bed; SM=Demosponge–*Megastrophia* bed; CCB=Cottage City Coral Beds; T=Tichenor Limestone; DR=Deep Run Member; M=Menteth Limestone; K=Kashong Member; W=Windom Member. Inset map shows locations of sections.

Creek (Loc. 5) in Genesee County and Cazenovia Creek (Loc. 1) in Erie County, the Hill's Gulch Bed rests on mudstones of the Wanakah Member. In Erie County, the Hill's Gulch Bed is, in turn, overstepped to the west by the widespread unconformity at the base of the Tichenor Limestone (Figure 6). Variable proportions of the Hill's Gulch Bed are removed by pre-Tichenor erosion in the several cutbanks on Cazenovia Creek, and it is completely missing downstream from Northrup Road. Southwestward from Cazenovia Creek, thin remnants of the Hill's Gulch Bed are present beneath the Tichenor Limestone in sections along the south branch of Smokes Creek near Windom. The Hill's Gulch Bed is absent at the Lake Erie shore (Baird, 1979). As such, this bed is the westernmost division of the Jaycox Member to be seen in outcrop.

In sections west of the Genesee Valley, the Hill's Gulch Bed contains corals, most notably large colonies of *Favosites hamiltoniae* which are sometimes overturned, with lesser proportions of *Eridophyllum* and *Heliophyllum*. The associated fauna is diverse and abundant, in particular the brachiopods *Mediospirifer*, *Pentamerella*, *Douwillina*, and *Rhipidomella*; bryozoans including *Sulcoretelpora*, fenestrate, and fistuliporoids; platyceratid gastropods; and the trilobite *Phacops*. Corals remain important in this unit eastward to Hill's Gulch, but east of Hill's Gulch they are much less common. From Hill's Gulch eastward, bivalves, including *Plethomytilus*, *Cypricardella*, *Modiomorpha*, *Actinopteria*, and *Pseudaviculopecten*, become important as the lithology changes to silty siliciclastic mudstone. East of the Genesee Valley, the brachiopods *Tropidoleptus* and *Mucrospirifer* become abundant as a result of muddier substrates; they dominate the fauna, and the overall biota becomes less abundant towards the east.

Post-Hill's Gulch mudstones and Tropidoleptus-Longispina beds.—The Hill's Gulch Bed grades upward into a sequence of sparsely fossiliferous, grey siliciclastic mudstone, treated herein as an unnamed division in the Genesee Valley-Hill's Gulch region (Figure 5). This unnamed division is traceable east into the Canandaigua Valley and is also recognizable in the Seneca Lake Valley. It is separated from the Hill's Gulch Bed by an intervening fossiliferous division herein designated the *Tropidoleptus-Longispina* interval (see Figures 5, 6). The post-Hill's Gulch mudstone interval is 30 cm thick at Hill's Gulch. It thickens to 50 cm at Jaycox Creek and expands to over 1.0 m in thickness in creeks west of Seneca Lake. The mudstone interval pinches out west of Hill's Gulch, where stratigraphic condensation places the Green's Landing Coral Bed on the top of the Hill's Gulch Bed (Figure 6).

The *Tropidoleptus-Longispina* fauna overlies the Hill's Gulch Bed from Bebee Creek (Loc. 10) in the Honeoye Lake Valley eastward into Seneca County. This 0.5 m-thick grey mudstone unit is characterized by the brachiopods *Tropidoleptus* and *Longispina*, which form conspicuous bedding-plane concentrations in the middle of the interval. Additional taxa include a small spiriferoid brachiopod, *Trematospira gibbosa*, and the gastropod *Platyceras*. Intact molt ensembles of the trilobite *Dipleura dekayi* and occurrences of the bivalve *Cypricardella* with splayed valves attest to rapid burial (abruption) events in this unit (Speyer and Brett, 1985; Allmon, 1985; see Brett et al., 1986).

Green's Landing Coral Bed.—Above the post-Hill's Gulch mudstone interval is a extremely fossiliferous soft, grey siliciclastic mudstone unit that commonly contains large corals (Figure 5). This unit was designated the "Green's Landing Coral Bed" by Mayer (1989) for exposures on an unnamed creek above Green's Landing at Canandaigua Lake (Loc. 13). This bed is traceable from Buffalo Creek (Loc. 2) in Erie County eastward into the Seneca Lake Valley (Figure 6). In eastern Erie County, the Green's Landing Coral Bed is overstepped by the

Tichenor Limestone; a 7 cm-thick basal remnant of this bed at Buffalo Creek is the westernmost outcrop of this unit (Figure 5). East of Buffalo Creek, this unit thickens to 54 cm at Murder Creek (Loc. 4) in Genesee County, but it thins to approximately 30 cm in the region between Hill's Gulch and Canandaigua Lake. This bed thickens to nearly 1.0 m in the vicinity of its type section before thinning again eastward to approximately 30-40 cm in creeks west of Seneca Lake.

The Green's Landing Coral Bed is the most prominent coral bed in the Jaycox Member. It contains a diverse array of benthic taxa similar to those described from coral beds in the overlying Windom Shale Member (see Baird and Brett, 1983). Large corals are common to abundant in this unit, from its western limit eastward into the Canandaigua Lake Valley. Large corals, including *Heliophyllum halli*, *Eridophyllum subcaespitosum*, *Cystiphyllum americanum*, *Favosites hamiltoniae*, and *F. argus*, are common, as is also the colonial morphotype *Heliophyllum halli* var. *confluens* (Figure 8A, B), which is particularly distinctive of this bed. Diverse brachiopods include the abundant taxa *Pentamerella*, *Douwillina*, *Elita*, *Parazyga*, and *Meristella*. Fenestrate and fistuliporoid bryozoans are abundant, as are the bivalves *Actinopteria*, *Cypricardina*, and *Pseudaviculopecten*. Abundant *Phacops*, pelmatozoan debris, and platyceratids are also usually present. Distinctive large (up to 1.5 cm diameter and 30 cm long), "rhizome-like," reptate hold-fast stems of camerate crinoids are found in this unit and in higher Jaycox shell beds. The Green's Landing Coral Bed is not well-developed in all places because of conspicuous spatial variations ("patchiness") in coral abundance and diversity. These variations occur along adjacent cutbanks of Jaycox Creek (Loc. 9) and between closely spaced creeks (see Hopewell Ravine, Loc. 12; Deep Run, Loc. 14).

Carbonate content and fossil density decrease eastward within this bed as the unit changes from an argillaceous limestone in Genesee County to a silty siliciclastic mudstone at Seneca Lake. The large corals are last observed in the Canandaigua Valley, where bivalves notably increase in abundance relative to the other groups. In the Seneca Lake Valley (Locs. 15, 16, and 17), the large corals are completely replaced by the small rugosans *Amplexiphyllum* and *Stereolasma*. East of Seneca Lake, essentially all of the corals have disappeared as this unit changes into a muddy siltstone (see below).

Mudstone interval above Green's Landing Coral Bed.—Above the Green's Landing Coral Bed at most localities in the Genesee Valley-Seneca Lake Valley region is a unit of variably fossiliferous and variably thick grey siliciclastic mudstone. This mudstone is absent west of Hill's Gulch and is nearly absent in sections immediately west of Seneca Lake (Figure 6; Locs. 15-17). This unnamed unit, which shows no directional thickness trend, reaches a maximum thickness of 78 cm west of Canandaigua Lake (Loc. 11), and generally contains a sparse fauna similar to that observed in the overlying Demosponge-Megastrophia bed discussed below (see Figure 9).

Demosponge-Megastrophia bed.—Overlying the Green's Landing Coral Bed at some sections and the post-Green's Landing mudstone interval at others, is a richly fossiliferous, calcareous to silty siliciclastic mudstone herein designated the "Demosponge-Megastrophia bed" for the distinctive occurrence of these taxa (Figures 5, 6). This bed is traceable eastward from the Bethany Center Dump roadcut to Seneca Lake (Figures 5, 6); it thickens eastward from 7.0 cm at Hill's Gulch to maximum thicknesses of 35-66 cm at localities in the Canandaigua Lake-Seneca Lake region. West of the Bethany Center Dump section, it becomes indistinguishable from older and younger beds as a result of westward stacking of thin, fossiliferous layers in the thin, condensed western sequence of the Jaycox Member.

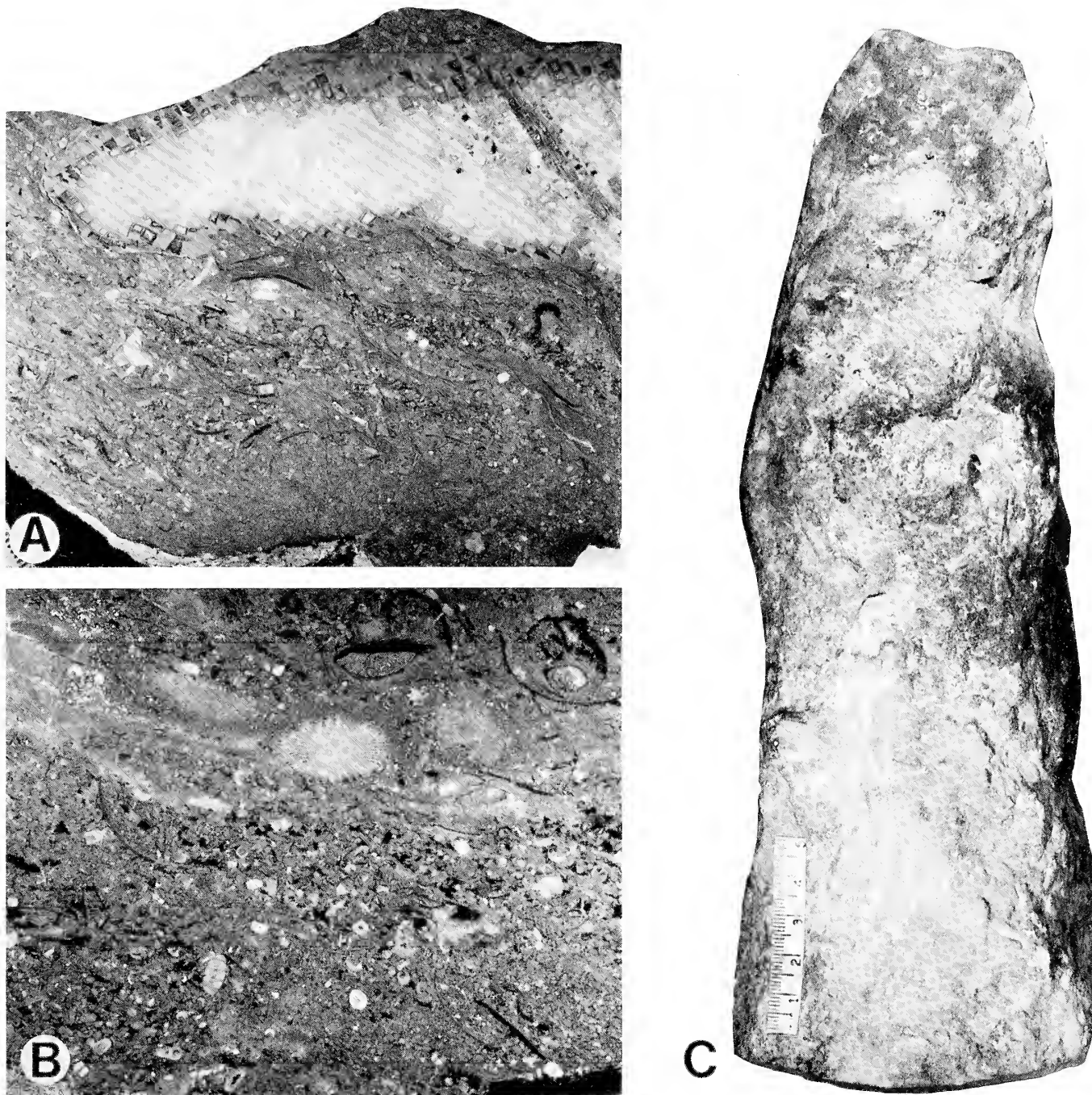


Figure 7. Polished slabs of basal Jaycox Member, Hill's Gulch Bed, showing crinoid packstone lithology; Buffalo Creek (Loc. 2). A, Slab showing crinoid packstone lithology; note *Favosites hamiltoniae* (tabulate, at top), rugose corals, and abundant trilobite debris (black); x1.0; NYSM 16469. B, Slab showing crudely developed grading of crinoidal grainstone into overlying coral-, brachiopod-, and trilobite-bearing packstone; x1.5; NYSM 16470. C, Prod-like burrow extending downward from base of Tichenor Limestone into Jaycox Member, Buffalo Creek (Loc. 2); x0.5; NYSM 16471.

The Demosponge–*Megastrophia* bed is characterized by numerous specimens of *Megastrophia concava*, a very large concavo-convex strophomenid brachiopod, and the occurrence of lithistid demosponges that are, as yet, undescribed (Figure 7). Other conspicuous organisms include mound-forming fistuliporoid bryozoans; large (up to 1.5 cm diameter) “rhizome-like” reptate, camerate holdfast structures; and occasional *Heliophyllum* and *Eridophyllum*. Common taxa include the brachiopods *Douvillina*, *Rhipidomella*, *Parazyga*, *Pentamerella*, and

Mediospirifer in association with fenestrate bryozoans, *Phacops*, and pelmatozoans. As with the underlying Hill's Gulch and Green's Landing Beds, there is an eastward drop in faunal diversity, abundance, and composition as the calcareous mudstone facies changes to calcareous silty mudstone. East of the Canandaigua Valley, large corals, the brachiopods *Megastrophia*, *Pentamerella*, *Parazyga*, and demosponges disappear, and *Tropidoleptus* and *Mucrospirifer* become abundant in this interval as a result of muddier conditions.

Middle Jaycox "barren" shale interval.—Above the Demosponge–*Megastrophia* bed and below the Cottage City Coral Beds is a very sparsely fossiliferous, grey siliciclastic mudstone interval (Figure 5) that is traceable from Hill's Gulch into the Canandaigua Valley (Figure 6). This interval, characterized by one or more thin calcareous mudstone beds interlayered with shale, thickens eastward from 62 cm at Hill's Gulch to almost 2.0 m at Hopewell Gully east of Canandaigua before thinning greatly to 40 cm at sections west of Seneca Lake (Figure 6). West of Hill's Gulch, this unit pinches out as the various Jaycox shell–coral beds become amalgamated by westward sedimentary condensation. As with other Jaycox units, this interval becomes somewhat siltier as it is traced eastward. Brachiopods from this unit include the large strophomenid *Mesoleptostrophia junia*, *Devonochonetes*, and *Mucrospirifer*. Other fossils include fenestrates, the trilobites *Phacops* and *Greenops*, and pelmatozoan debris.

Cottage City Coral Beds.—The highest fossil-rich unit of the Jaycox Member is an interval of thin beds usually rich in large rugose and tabulate corals (Figures 4B and 5). This interval is herein designated the "Cottage City Coral Beds" for exposures on Deep Run (Loc. 14) north of Cottage City on the east side of Canandaigua Lake (Figure 3). At this type section, the unit is a 93.5 cm-thick interval marked by two coral-bearing beds interspersed with calcareous mudstone rich in brachiopods, bryozoans, and pelmatozoan debris. The Cottage City Coral beds are traceable from Hill's Gulch eastward at least as far as Seneca Lake (Figure 5 and 6). West of Hill's Gulch, this unit is overstepped by the sub-Tichenor disconformity, and it is absent in sections west of there (Figure 5 and 6). This unit thickens erratically eastward from 35 cm at Hill's Gulch to a maximum of 207.5 cm at Hopewell Gully east of Canandaigua, before thinning to less than 1.0 m in sections west of Seneca Lake. In general, the uppermost bed in this interval is richest in fossils and contrasts strongly with the fossil-poor facies of the overlying Benton Run Mudstone.

The Cottage City Coral Beds are similar in facies to the Green's Landing Coral Bed, with two exceptions. *Heliophyllum halli* var. *confluens* has not been found in the upper coral beds, and *Cystiphyllodes* is a more abundant coral than in the Green's Landing Coral Bed. In addition, the uppermost ledge of the Cottage City Coral Beds is usually more calcareous, siltier, and harder than the mudstones in the Green's Landing Coral Bed. *Cystiphyllum*, *Heliophyllum*, *Eridophyllum*, and *Favosites* are the important corals; *Douvillina*, *Pentamerella*, *Elita*, and *Parazyga* are common brachiopods; and fenestrates and fistuliporoids are the key bryozoans. Large stoloniferous camerate holdfasts are characteristic of this unit, as well as in the underlying middle Jaycox coral–shell beds. As with other Jaycox shell beds, the large corals are replaced by the small rugose genera *Amplexiphyllum* and *Stereolasma* in Seneca Lake Valley localities, and the brachiopods *Tropidoleptus* and *Productella*, typically associated with siliciclastic mudstone facies, become important within this interval in this region.

Benton Run Mudstone.—The highest Jaycox division, present from Hill's Gulch eastward into the central Finger Lakes region, is a sparsely fossiliferous, calcareous, silty grey siliciclastic mudstone herein designated the "Benton Run Mudstone" for exposures along the main channel of Benton Run (Loc. 15) at Seneca Lake. This unit thickens gradually eastward from 5 cm at Hill's Gulch to 55 cm at the west shore of Canandaigua Lake (Loc. 11). It thickens even more rapidly to the south. At Hopewell Ravine, this unit is only 45 cm thick, but at the Tichenor Limestone-capped falls in the main channel of Deep Run, 9.0 km southwest of Hopewell Ravine, it is 82 cm thick, and in the south tributary of

Deep Run it is 1.3 m. Moreover, at the type section along Benton Run, west of Seneca Lake and 20 km southeast of Hopewell, this interval increases to 5.0 m. At Kashong Glen, 4 km south of Benton Run, it is 7.4 m.

Much of the northward and westward thinning of this unit appears to be due to erosional truncation of the Jaycox Member below the sub-Tichenor disconformity, but a second factor appears to be northwestward sedimentary condensation, a pattern clearly visible in underlying Jaycox beds and also conspicuous in the overlying Tichenor Limestone–Menteth Limestone succession in the same region (see Baird, 1979; Baird and Brett, 1981). East of Canandaigua Lake, the uppermost few decimeters of the Benton Run Mudstone become notably silty, and in the Seneca Lake Valley the uppermost part of the unit beneath the Tichenor has changed into a thin-bedded, *Zoophycos*-rich, muddy siltstone facies.

Although the fauna is meager in the Benton Run Mudstone, there are a few common forms; these include the brachiopods *Devonochonetes*, *Mucrospirifer*, *Mediospirifer*, *Athyris*, *Mesoleptostrophia*, *Tropidoleptus*, and *Meristella*. The trilobite *Greenops boothi*, several bivalve genera, and pelmatozoan debris occur at several levels. In the three sections (Locs. 15, 16, and 17) west of Seneca Lake, a large variant of the tabulate coral *Pleurodictyum americanum* occurs in a meter-thick interval approximately 30 to 90 cm above the base of this unit.

Stratigraphy of the Spafford and Jaycox Members: Seneca Valley–Skaneateles Valley region

Revised upper Ludlowville Formation correlations

Recent detailed mapping of strata previously included in the "King Ferry Member" shows that some units of the Spafford and Jaycox Members can be traced between Kashong Glen (Loc. 16) and the Skaneateles Valley. These members, therefore, can be extended westward and eastward, respectively, to include the upper "King Ferry" beds in the Seneca–Owasco Valley region (Mayer et al., 1990; Figure 7). The Jaycox Member is progressively beveled below the sub-Tichenor disconformity southeastward across the Cayuga, Owasco, and Skaneateles Valleys, and only the Spafford Member is present at the southeast ends of the Cayuga and Tully Valleys.

The Limerick Road Bed can be traced into the Cayuga Valley, where it apparently becomes amalgamated with the underlying Bloomer Creek Bed. The overlying "barren" mudstone interval is found to be entirely correlative with the Spafford Member in central New York, and the Hill's Gulch Bed correlates with the Owasco Siltstone in central New York (see Figures 8 and 9).

Spafford Member

Limerick Road Bed.—The Limerick Road Bed is traceable into the Cayuga Valley and assumes a condensed character from Kashong Glen eastward to Big Hollow Creek (Loc. 19) near Romulus, Seneca County, and in sections along the west side of Cayuga Lake (Figures 9 and 10). Erosion below this bed is shown by the occurrence of exhumed carbonaceous concretions derived from dark grey shales of the underlying Wanakah Member; some of these concretions display *Trypanites* borings, and a few are encrusted by *Pleurodictyum* and pelmatozoan holdfasts (Figure 10A) in a manner similar to reworked concretions in the Bloomer Creek Bed of the underlying Wanakah ("King Ferry") Member in this region (see Baird, 1981). The lower 20 cm of the

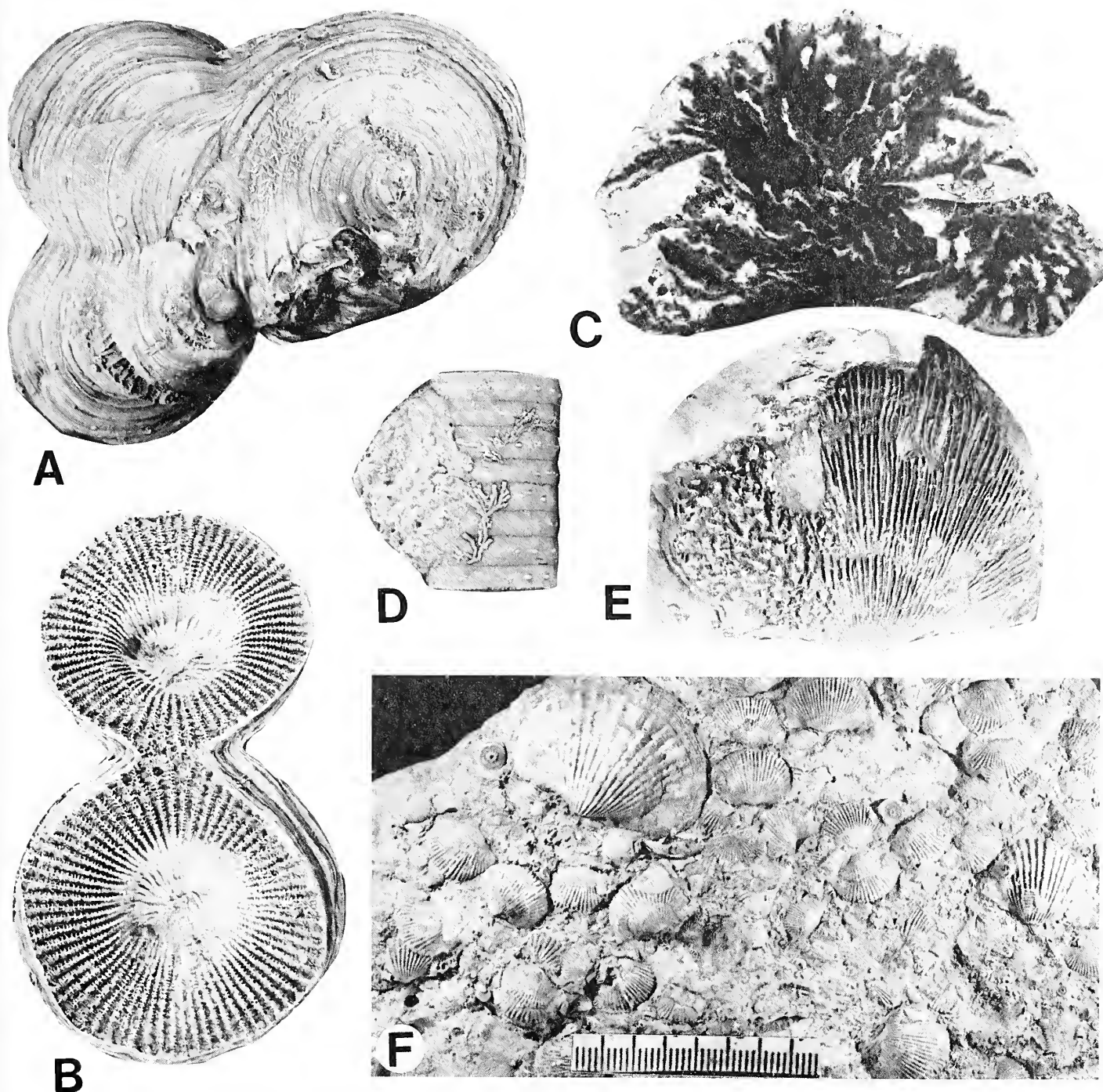


Figure 8. Representative fossils of Jaycox Member in western New York. All specimens except 7F from south fork of Jaycox Creek, near Geneseo, Livingston County, New York (Loc. 9). A, B, *Heliophyllum halli* var. *confluens* Hall; basal and calyx views of weakly colonial rugose coral typical of Green's Landing Coral Bed; x1.0; NYSM 16472, 16473. C, Polished cross-section of unidentified lithistid demosponge typical of Demonsponge–*Megastrophia* bed of Jaycox Shale, x1.5, NYSM 16474. D, Large columnar of camerate crinoid encrusted by unidentified demosponge (left) and *Hederella* bryozoan (center); Demonsponge–*Megastrophia* bed; x1.5; NYSM 16475. E, Brachiopod *Megastrophia concava* (Hall) with attached demosponge; x1.5, NYSM 16476. F, Slab of typical *Tropidoleptus carinatus*–*Longispina mucronatus*-bearing shale from lower Jaycox Member, Deep Run gully, Canandaigua Lake, Ontario County, New York (Loc. 12); x1.0, NYSM 16477.

Limerick Road Bed above the disconformity has large *Pleurodictyum* and occasional *Athyris*, *Mucrospirifer*, and *Mediospirifer*, as well as molluscan debris that includes numerous orthoconic nautiloids. The latter are commonly encrusted by *Reptaria stolonifera*, a bryozoan that may have been commensal on the living nautiloid (see Baird et al., 1989).

Dark grey shale of the Wanakah Member (Romulus beds), with bedding-plane concentrations of diminutive *Ambocoelia umbonata* var. *nana*, *Truncalosis truncata*, and *Tropidoleptus*, is directly overlain by diastemic debris of the Limerick Road Bed at Kashong Glen, at an unnamed creek in Sampson State Park (Loc. 18) and at Big Hollow Creek (Loc. 19). Farther southeast at Mack Creek (Loc. 20) and at

Barnum Creek (Loc. 22), recognition of the Limerick Road Bed becomes difficult as the diminutive brachiopod beds of the upper Wanakah Member either greatly thin or are truncated in the southeast direction (Figures 2 and 9). In the vicinity of Sheldrake, Seneca County (Loc. 26), and Aurora, Cayuga County (Loc. 27), the Limerick Road Bed may lie directly on the Bloomer Creek Bed of Baird (1981), and forms a conspicuous regional marker at the base of the Spafford Member in central New York (Figure 2; Brett et al., 1986). Hence the Limerick Road Bed appears to be correlative with the basal part of the Spafford Member.

"Barren" mudstone division above Limerick Road Bed.—East of Kashong Glen, the Spafford-equivalent "barren" mudstone interval continues to thicken eastward and southeastward from approximately 1.8 m

west of Seneca Lake to approximately 7.5 m at most Cayuga Valley localities (Figure 9). At the Ludlowville type section and at Portland Point (Locs. 29 and 30) north of Ithaca in the Owasco-Tully Valley region, beds equivalent to this unit make up most to nearly all of the upper Jaycox Member. These fossiliferous, silty grey mudstones resemble the type Spafford Member, a unit originally described by Smith (1935) at sections both within and east of the Skaneateles Valley.

As at sections west of Seneca Lake, the Spafford Member in the Seneca and Cayuga Lake areas contains a very sparse fauna with occasional chonetids, bivalves, and indistinct trace fossils, but it is much thicker and slightly siltier. However, one major difference is the presence of abundant, compressed, 1.0-1.5 cm (average diameter) discoidal impressions of a membranous problematic organism (Figure 10C) in

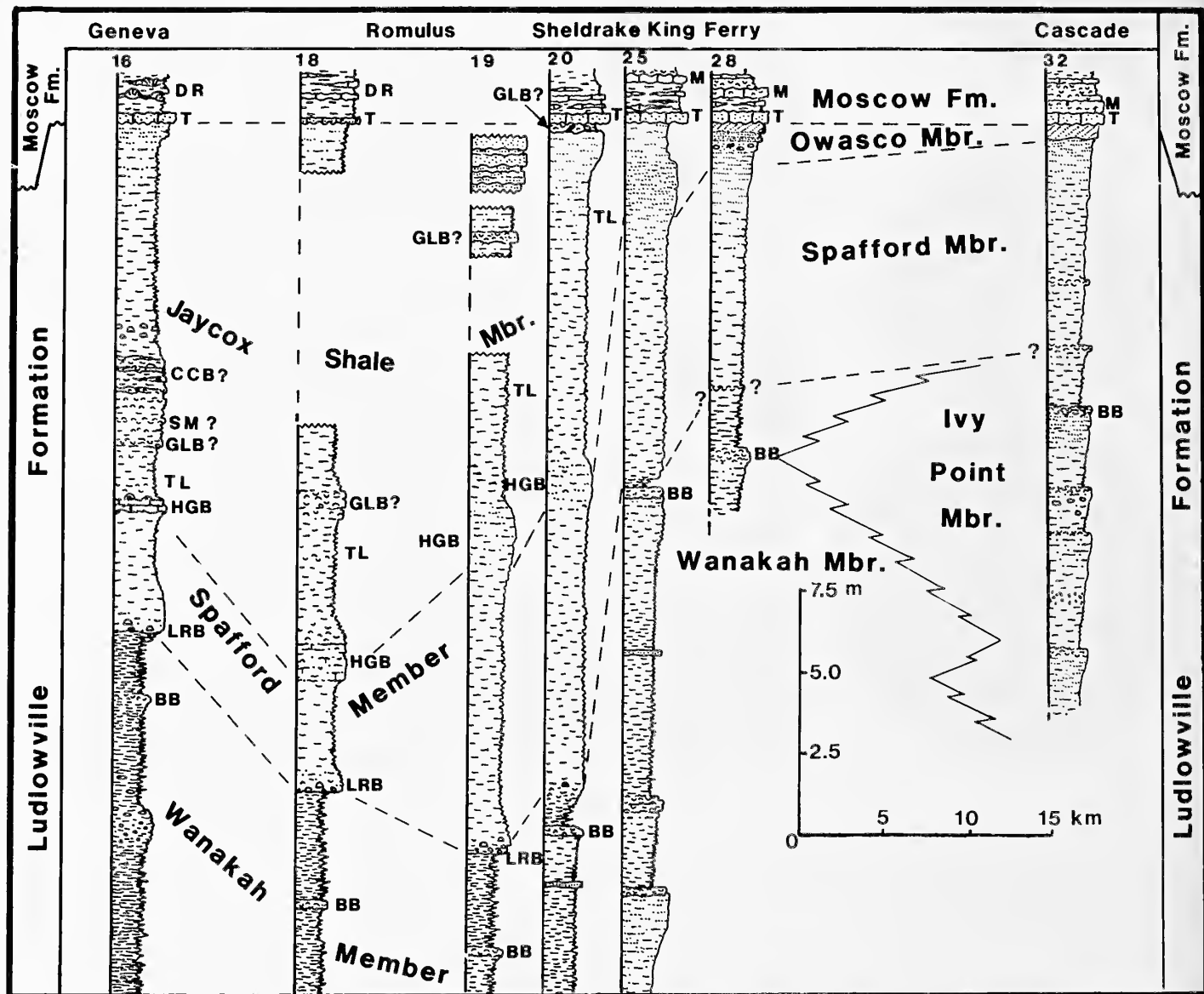


Figure 9. Correlation of units in the Spafford and Jaycox Members and Owasco Siltstone (Ludlowville Formation) within the Seneca Lake, Cayuga Lake, and Owasco Lake Valleys. Units include BB=Bloomer Creek Bed; LRB=Limerick Road Bed; HGB=Hill's Gulch Bed; TL=Tropidoleptus-Longispina mudstone interval; GLB=Green's Landing Coral Bed; SM=Demosponge-Megastrophia bed; CCB=Cottage City Coral Beds; T=Tichenor Limestone; DR=Deep Run Member; W=Windom Member.

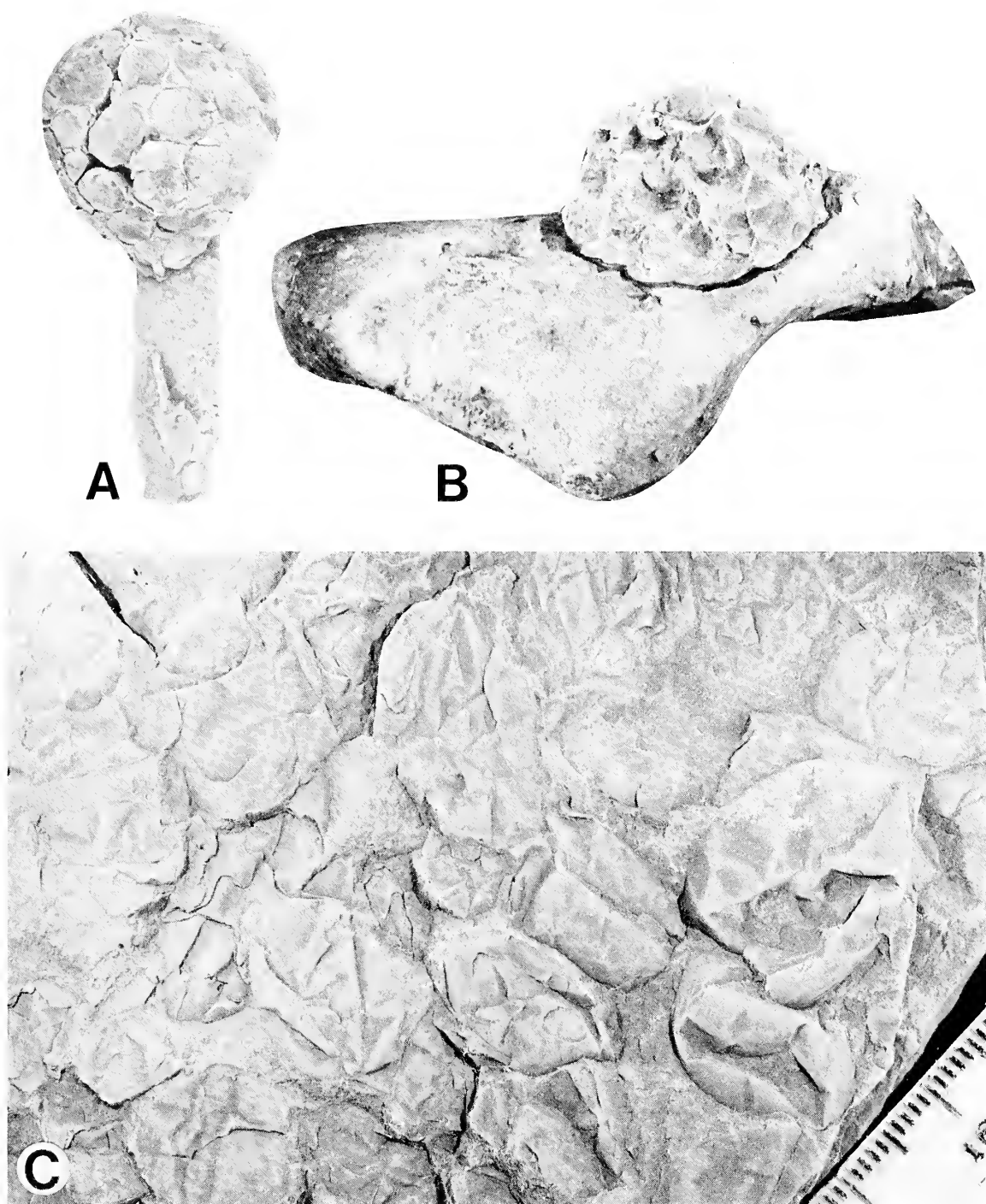


Figure 10. Fossils from lower part of Spafford Member in the Cayuga-Seneca Lake area. *A, B*, Reworked concretions with encrusting *Pleurodictyum*, Limerick Road Bed; x1.0. *A*, Big Hollow Creek near Romulus, Seneca County, New York (Loc. 19); NYSM 16478. *B*, Creek at Sampson State Park, Seneca County, New York (Loc. 18); NYSM 16479. *C*, Slab of shale about 1.0 m above Limerick Road Bed with abundant discoidal fossils of unknown affinities; these problematical fossils are diagnostic of the lower Spafford "barren" mudstone interval in the central Finger Lakes region. Big Hollow Creek, near Romulus, Seneca County, New York (Loc. 18); x1.5; NYSM 16480.

the lower 1.5 to 2.0 m of this unit, at localities as far west as Kashong Glen (Loc. 16; immediately above the Limerick Road Bed) to the Ludlowville type section (Loc. 29). These discoidal remains occur locally as far east as the Skaneateles Valley (in the middle Spafford Member), but they are much less common and poorly preserved in these areas. They occur as dense concentrations of compressed disks

that usually have a four- to six-rayed pattern of pleats, which were evidently produced as an artifact of compression and/or desiccation (Figure 10C).

The discoidal fossils occur on numerous, but not all, bedding surfaces within their vertical stratigraphic range. Deposits containing dense concentrations of these objects are notably silty and laminated.

Moreover, deposits yielding these enigmatic fossils contain virtually no other macrofossils except for large *Pleurodictyum* and peculiar rod-like endichnial burrows at many levels. The biological affinities of these disks are unknown, but intervals with abundant disks are a special facies that records rapid bottom-smothering (obration) events. Thus these beds offer the potential for discovery of other soft-bodied or lightly sclerotized organisms.

Between Kashong Glen (Loc. 16) and Sheldrake Creek, Seneca County (Loc. 26), the base of the Spafford Member is the Limerick Road discontinuity-debris Bed. However, southeast of the vicinity of Sheldrake, the Limerick Road Bed is no longer discernible, and the "barren" mudstone interval appears to rest on the Bloomer Creek Bed, an important upper Wanakah marker bed separated from the "barren" mudstone by intervening uppermost Wanakah beds (Romulus diminutive brachiopod beds) farther northwest (Figure 9). Evidently, the diminutive brachiopod-bearing shales of the upper Wanakah Member, or Romulus Beds (Brett et al., 1986), have disappeared to the southeast as a result of either overstep by the Limerick Road Bed or pinchout along the northwest-facing paleoslope that was present in that area during Bloomer Creek Bed deposition (Baird, 1981; Baird and Brett, 1981). If the latter model is appropriate, then some beds in the lower Spafford Member may also have lapped out on this surface. At any rate, no vestige of the uppermost Wanakah Member (Romulus Shale) remains at Sheldrake, and the basal contact of the Spafford Member appears to be merged (amalgamated) into the complex meter-thick interval of shell-debris layers of the Bloomer Creek Bed. These stratigraphic relationships are maintained across the eastern Finger Lakes region (Figures 2 and 9).

Spafford Member: Central New York fossiliferous mudstones.—The eastward transition between "barren" mudstone and laterally equivalent 7 to 8 m-thick fossil-rich facies of the Spafford Member is best preserved in the Cayuga and Owasco Valleys. The "barren" mudstone, including the interval with the problematical disks, grades eastward into mudstone facies with the brachiopods *Schuchertella*, *Devonochonetes scitulus*, *D. coronatus*, *Longispina*, *Athyris*, *Pseudoatrypa*, *Tropidoleptus*, *Spinocyrtia*, *Orthospirifer*, and *Mucrospirifer* at Salmon Creek (Loc. 29) near Portland Point and at Cascade (Loc. 32) along Owasco Lake. At these sections, *Pleurodictyum*, the bryozoan *Sulcoretepora*, and the bivalves *Grammysia*, *Modiomorpha*, and *Orthonota* occur. Although the fauna becomes somewhat more abundant and diverse in the Skaneateles Valley, the biota at Salmon Creek and Cascade is sufficiently rich to resemble that of the typical Spafford Member farther east (Figures 2, 11, and 13).

Jaycox Member

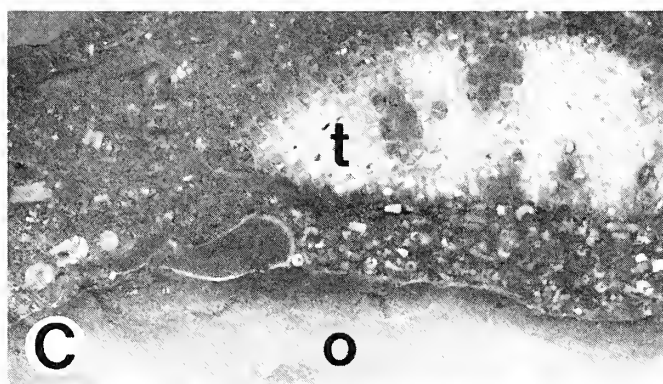
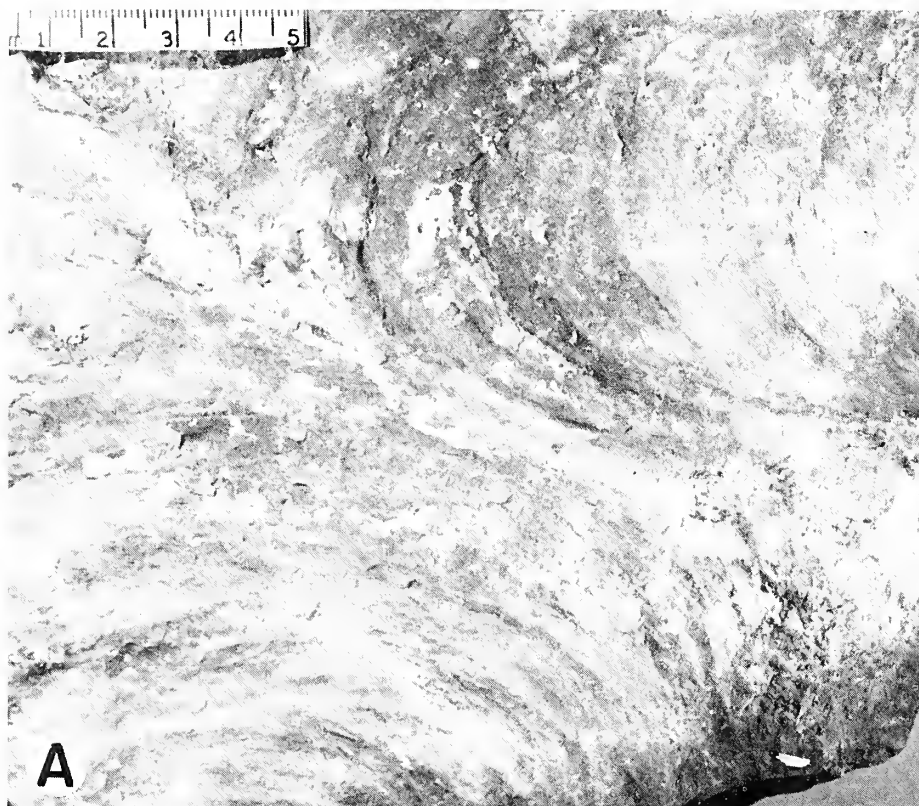
Hill's Gulch Bed–Owasco Siltstone correlation.—The Hill's Gulch Bed grades southeastward into the Owasco Siltstone through a transitional belt of thickened silty mudstone to muddy siltstone facies that is essentially coincident with the axis of the Romulus Sag (Figures 9, 12). In the Jaycox Creek–Kashong Glen region, the Hill's Gulch Bed

becomes progressively less calcareous, less fossiliferous, and siltier in the eastward direction. From Kashong Glen to Big Hollow Creek, this unit thickens into a silty, calcareous, siliciclastic mudstone that is differentiable from the overlying and underlying beds by its more calcareous character and somewhat greater fossil content (Figures 9 and 13). Southeastward from Big Hollow Creek, this mudstone interval both thins and coarsens so that, near Barnum Creek, it becomes a muddy siltstone with abundant *Zoophycos* and *Tropidoleptus*. Near Sheldrake Creek, this facies grades into a thin-bedded, fine silty sandstone with abundant shells of the brachiopod *Allanella* ("*Spirifer*") *tullius* and *Zoophycos* (Figure 11). Because of the similarity of this facies to the typical siltstone facies of the Owasco Siltstone, in the Owasco Valley and farther east (see Smith, 1935) the Owasco Siltstone is redefined herein to include Hill's Gulch-equivalent strata at all Cayuga Valley sections to the south and east of Glenwood Point ravine, 1.0 km north of King Ferry, Cayuga County (Figures 12 and 13). Farther to the southeast, this unit thins as a result of condensation and erosional overstep following development of the sub-Tichenor disconformity (Figure 13). Southward from an east-northeast to west-southwest line between Sheldrake, Seneca County, and Aurora, Cayuga County, this unit is progressively truncated from above, so that no Owasco strata are present at either Salmon Creek (Loc. 29) or Portland Point (Loc. 30) (Figures 13 and 14). In the Owasco, Skaneateles, and Tully Valleys, there is also a trend of southeastward thinning of the Owasco Siltstone, although the northwest to southeast outcrop belt suitable for tracing this unit within each valley is much less well-developed than in the Cayuga Valley (see Figures 7, 8). At Ensenore Ravine (Loc. 31), the Owasco Siltstone is 1.3 m thick, distinctly thin-bedded, and silty, but at Cascade (Loc. 32), only 2.0 km farther southeast, the unit has become much more thick-bedded and sandy and is only 65 cm thick. At the southernmost Jaycox-equivalent section in the Skaneateles Valley, the Owasco Siltstone is only 12 cm thick, and at Fellows Falls in the Tully Valley it is nearly absent.

At Sampson State Park and at Big Hollow Creek, the Hill's Gulch Bed contains numerous *Devonochonetes*, *Tropidoleptus*, and *Mucrospirifer*, as well as bivalves and scattered pelmatozoan ossicles. Southeast of Big Hollow Creek, these elements persist, but the trilobite *Dipleura* makes its appearance as the lithology turns to *Zoophycos*-swirled siltstone. "*Allanella*" and pteriod bivalves eventually dominate the biota as the facies grades southeastward into cross-laminated fine-grained sandstone that appears in the vicinity of Sheldrake–Black Rock and King Ferry.

In Cayuga Valley localities, the Hill's Gulch Bed and equivalent Owasco Siltstone are transitional downward and upward into mudstones, except where the Owasco Siltstone is disconformably overlain by the Tichenor Limestone. However, in the Owasco, Skaneateles, and Otisco–Tully Valley region, the Owasco Siltstone has a sharp, apparently erosional, basal contact with the Spafford Member (Figure 9); rip-up clasts are sometimes observed within the basal Owasco Siltstone, and

Figure 11. Fossils from Spafford Member and Owasco Siltstone, Cayuga Lake–Skaneateles Lake region. A, Bedding-plane in Owasco Siltstone with well-defined spreiten of *Zoophycos*; Rte. 38 roadcut, Cascade, Cayuga County, New York (Loc. 38); x0.75; NYSM 16481. B, Laterally compressed specimen of the trilobite *Dipleura dekayi* (Green) in transitional Owasco Siltstone; unnamed creek south of Powell Creek near Sheldrake, Seneca County, New York; x1.0; NYSM 16481. C, Polished section of Owasco Siltstone (O) showing sharp contact with overlying Tichenor Limestone (T); Rte. 38 roadcut at Cascade, Cayuga County, New York (Loc. 38); NYSM 16482. D, Slab of Owasco Siltstone with numerous molds of the brachiopod *Allanella tullius* (Hall), Spafford Landing, Skaneateles Lake, Onondaga County, New York; x1.6; NYSM 16484. E, Typical slab of Spafford Member with abundant molds of brachiopods and bivalves; creek near Spafford Landing, Skaneateles Lake, Onondaga County, New York (Loc. 34); x1.0; NYSM 16483.



the cross-laminated facies of the Owasco contrasts strongly with the bioturbated, (non-tractional?) silty mudstone beds of the upper Spafford Member. This southeastward erosional downcutting of Spafford beds by the medium- to high-energy depositional environments of the Owasco Siltstone is not surprising. However, it is particularly significant that this downcutting is a "mirror image" of the progressive westward truncation of Spafford deposits ("barren" shale interval and Limerick Road Bed) by the Hill's Gulch Bed across Genesee County (see Figure 5).

Middle Jaycox shell-coral-rich interval.—The interval between the Hill's Gulch Bed and the Benton Run Mudstone interval, which includes conspicuous coral beds in western New York, loses much of its remaining biota of corals, diverse brachiopods, fistuliporoid bryozoans, and large pelmatozoan fossils as it is traced eastward to the vicinity of Romulus, Seneca County. At Sampson State Park and at Big Hollow Creek, this interval is poorly exposed and cannot be measured completely. Sampson State Park, which is the more complete of the two sections, is the easternmost locality with the characteristic diverse fauna. This diverse fauna occurs in a silty siliciclastic mudstone interval approximately 3.0 m above the top of the Hill's Gulch Bed (Figure 7). This resistant unit is 0.75 m in thickness, but its top is not exposed. Beneath it, the characteristic *Tropidoleptus*–*Longispina* mudstone interval occurs in the upper half of the mudstone sequence that separates the Hill's Gulch Bed from the fossil-rich silty mudstone unit.

At Big Hollow and Mack Creeks, the *Tropidoleptus*–*Longispina* interval is still recognizable, but a structurally isolated overlying

sequence of thin-bedded, bioturbated, *Zoophycos*-rich siltstone is present above the *Tropidoleptus*–*Longispina* mudstone at Big Hollow Creek. This siltstone possibly represents deposits of the Jaycox Member above the Green's Landing Coral Bed in this area. Just below the siltstone interval at Big Hollow Creek is a thin pelmatozoan- and bryozoan-rich bed that may be the Green's Landing Coral Bed (Figures 9 and 13). Unfortunately, strata both below the pelmatozoan- and bryozoan-rich bed and above the overlying siltstone unit are concealed at this section; the limited exposure makes it impossible to observe the precise position of this bed relative to the rest of the Jaycox Member and to the Tichenor Limestone. It is possible, however, that the siltstone interval occurs just beneath the Tichenor at this section, because this unit is essentially absent at Mack Creek, the next section southeast of Big Hollow Creek. At Mack Creek, only 15 cm of a unit rich in *Eridophyllum*, *Favosites*, and *Heliophyllum* is present below the sub-Tichenor disconformity and above the 5.0 m-thick *Tropidoleptus*–*Longispina* interval (Figure 13); this coral-rich bed may be the easternmost outcrop of the Green's Landing Coral Bed, but this interpretation remains speculative. At Barnum Creek 3 km farther to the southeast, only the lower part of the *Tropidoleptus*–*Longispina* interval occurs above the Hill's Gulch Bed as a result of conspicuous, rapid, southeastward overstep of the Jaycox Member beneath the sub-Tichenor disconformity (Figures 13 and 14). Strata within the Owasco Siltstone and Spafford Member are present in sections at, and southeast of, Sheldrake Ravine (Figure 14).

Benton Run Mudstone.—East of Kashong Glen and adjacent sec-

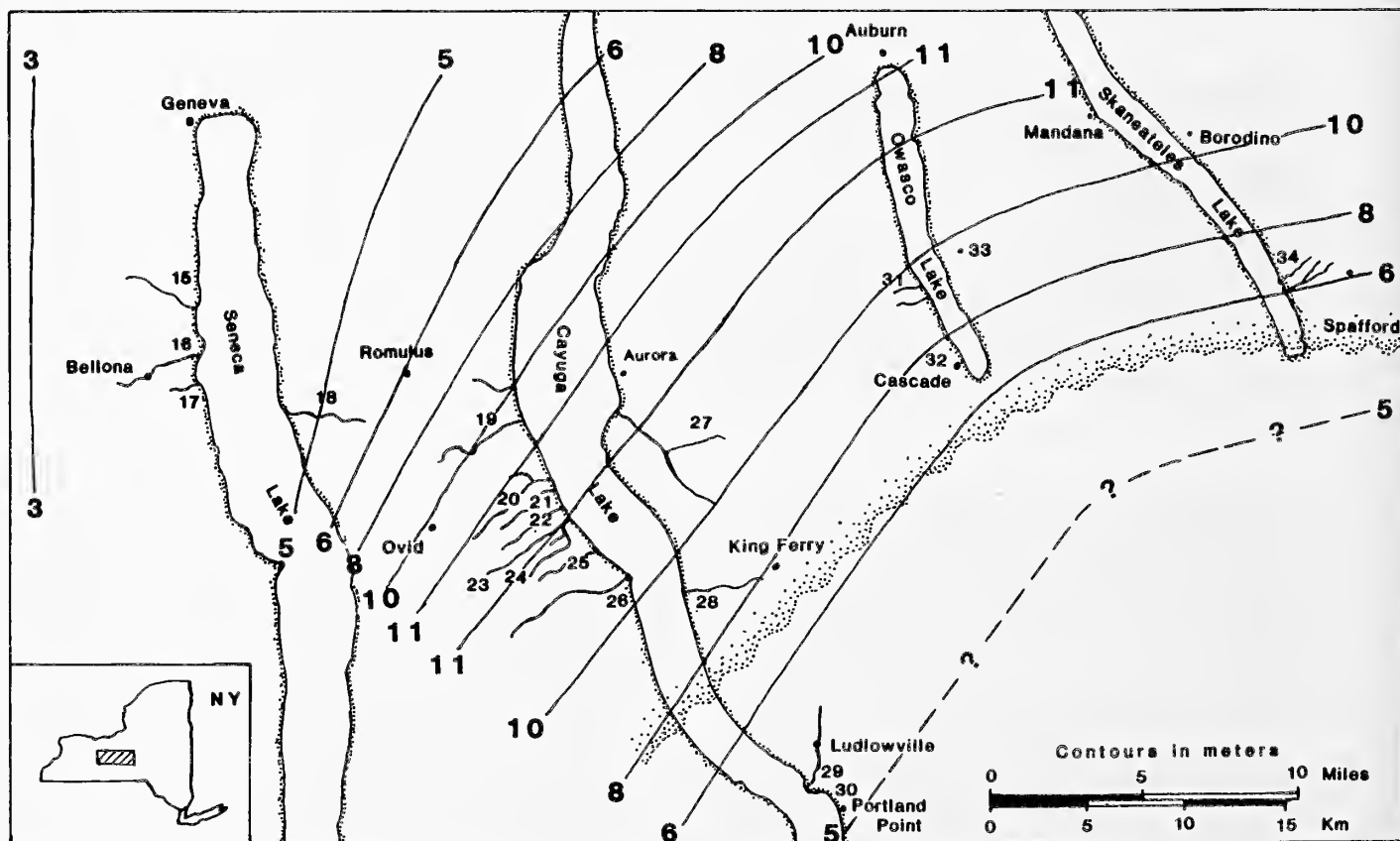


Figure 12. Isopach map of Spafford Member and Owasco Siltstone in the central Finger Lakes area. Numbers refer to locations listed in Appendix I. Stippled area in southeast indicates region of truncation of Owasco Siltstone by pre-Tichenor erosion; dashed contour line (5.0 m) indicates approximate thickness of partially truncated Spafford Member.

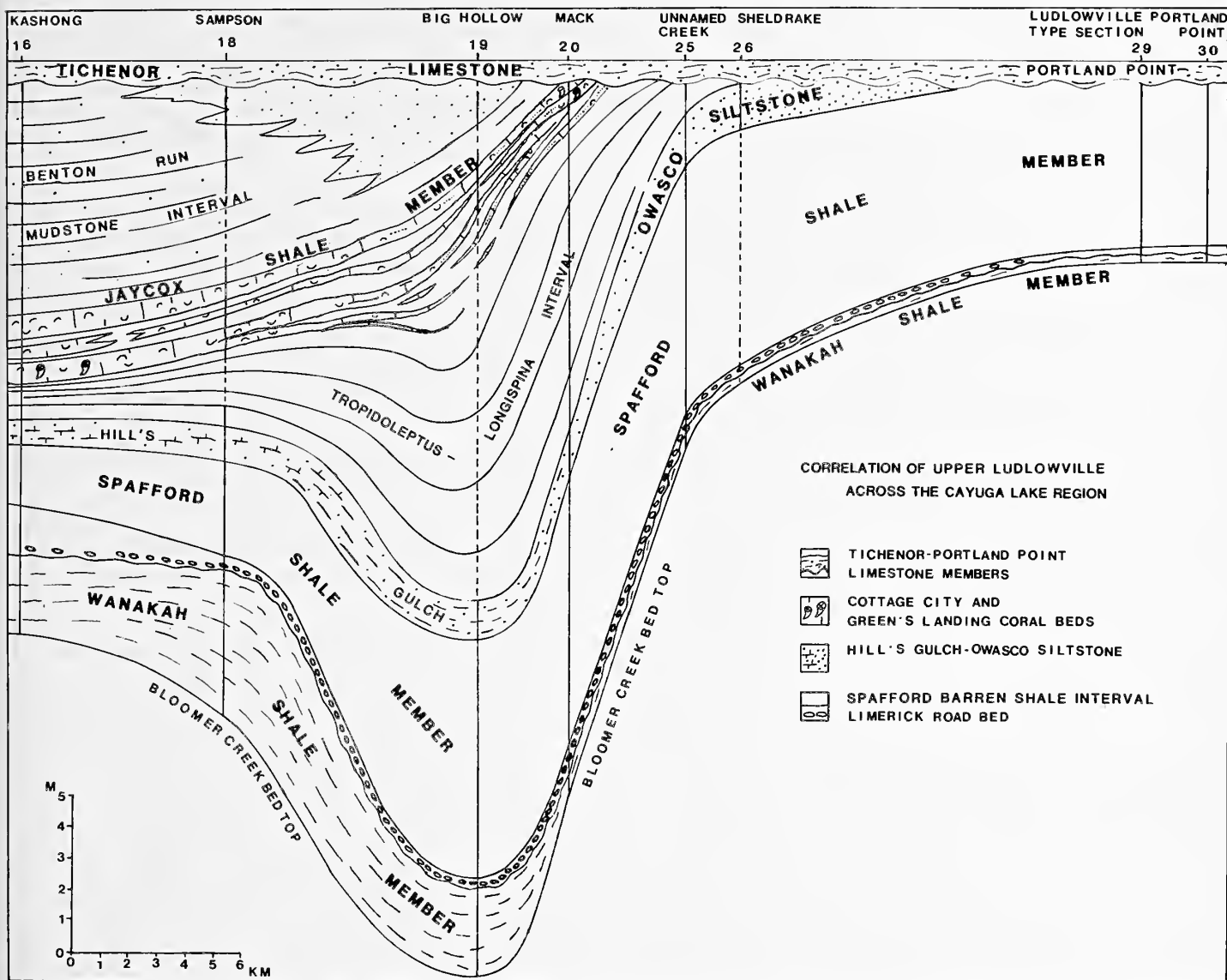


Figure 13. Schematic northwest/southeast cross-section of upper Ludlowville Formation from Seneca Lake to southeastern Cayuga Lake. Note dramatic thickening toward Big Hollow Creek; also note southeastward truncation of Jaycox units that juxtaposes Tichenor Limestone onto the Spafford Member.

tions along Seneca Lake, the Benton Run Mudstone apparently thins somewhat toward Sampson State Park, where it is only partly exposed. East of the latter locality, the Benton Run Mudstone thins towards Big Hollow Creek, where it is represented by a silty mudstone and siltstone sequence below the probable Tichenor-equivalent, or is completely absent as a result of eastward-southeastward erosional overstep below the sub-Tichenor disconformity (Figures 9 and 13). If Benton Run-equivalent beds are present at Big Hollow Creek, they are represented by the *Zoophycos*-rich siltstone interval and additional underlying mudstone beds. However, if the siltstone interval is the eastern equivalent of the Cottage City Coral Beds and/or lower fossil-rich beds above the Green's Landing Coral Bed (see discussion above), then the Benton Run Mudstone interval is missing at Big Hollow Creek. Strata above the siltstone interval are not exposed at this creek, and this leaves some ambiguity as to the nature and thickness of the upper Jaycox Member in this area.

Blocks of Tichenor Limestone in the bed of Big Hollow Creek

upstream from the problematic siltstone suggest that this siltstone unit occurs near the base of the Tichenor, although not necessarily at its base. If this interpretation is correct, then the Benton Run Mudstone interval is certainly absent at Mack Creek farther to the southeast, where only a thin coral-rich unit appears beneath the Tichenor Limestone and above the *Tropidoleptus*-*Longispina* mudstone interval.

At Kashong Glen, adjacent creeks west of Seneca Lake, and Sampson State Park, the Benton Run Mudstone, interval is largely a nondescript sequence of silty grey to dark grey mudstone, with a sparse brachiopod fauna composed of *Tropidoleptus*, *Mucrospirifer*, *Devonochonetes scitulus*, and *D. coronatus*. The tabulate corals *Pleurodictyum* and *Thamnoptychia*; the bivalves *Modiomorpha*, *Modiomorpha*, *Grammysia*, *Cypricardella*, and *Orthonota*; and the trilobite *Greenops* also occur. As the Benton Run Mudstone interval grades upward into a 0.5 m-thick interval of thin-bedded siltstone immediately below the Tichenor Limestone, its fauna picks up large pteriod bivalves and the fodinichnial trace *Zoophycos*. These latter ele-

ments are particularly abundant in the problematic siltstone interval at Big Hollow Creek, to which the Benton Run Mudstone interval may be equivalent.

Spafford-Jaycox biofacies

Biofacies classification scheme

Brett et al. (1986, 1990) and Vogel et al. (1987) outlined a classification of biofacies groupings for the Middle Devonian Hamilton Group that is used herein (Figures 15 and 16). Key associations in this classification are believed to be controlled by two main overlapping variables, both with implied paleoenvironmental controls. They are: (1) bottom oxygenation (depth), and (2) turbidity (sediment influx and sedimentation rate). Although biofacies in the underlying Wanakah Member were strongly influenced by bottom oxygenation levels (see Baird, 1981; Baird and Brett, 1981; Miller, 1986, 1991; Miller et al., 1988), the main paleoenvironmental stress factors for Spafford and Jaycox organisms were turbidity, storm turbulence, and bioturbation-induced trophic amensalism.

For purposes of lithofacies-biofacies generalizations, the western New York Spafford-Jaycox Member interval can be separated vertically into three divisions that reflect two overall paleoenvironmental conditions. The mudstone-rich Spafford Member records predominantly turbid conditions and an unstable substrate. The shell-rich Green's Landing Coral Bed through Cottage City Coral Beds sequence of the

Jaycox Member records intervals of reduced turbidity and implied lower sediment accumulation rates. The Benton Run Mudstone records a return to more turbid conditions with unstable substrates. Facies of the Hill's Gulch Bed grade west of the Genesee Valley, where they exhibit lower sedimentation rates. Together with the Green's Landing Coral Bed, these units comprise the condensed far-western Jaycox sections (see Mayer, 1989).

Biofacies of the Jaycox Member

In the western New York region, the Jaycox Member features either all or some of the six biofacies units in the classification (see Figure 15 for list of key taxa in the Jaycox biofacies scheme). Jaycox Member mudstones include the upper part of the *Athyris* field and all of the *Tropidoleptus* field. Jaycox shell-coral beds encompass the *Favosites hamiltoniae* and *Pentamerella-Heliophyllum*, and parts of the diverse brachiopod and the *Tropidoleptus* biofacies fields (Figure 16A-C, E). The *Favosites hamiltoniae* biofacies records firm-bottom, clear-water conditions at or just below the limit of fair-weather wavebase (Brett et al., 1986, 1990). The *Pentamerella-Heliophyllum* association (Figure 16C) records lower energy, firm, muddy-bottom conditions on the infralittoral shelf bottom under conditions of low net sediment supply. The diverse brachiopod field (Figure 16A) records firm, muddy-bottom conditions near the lower limit of storm-wave impingement (Brett et al., 1986, 1990).

Shelly deposits of the Jaycox Member display faunal changes as they are traced eastward into thicker silty facies; one of these is the

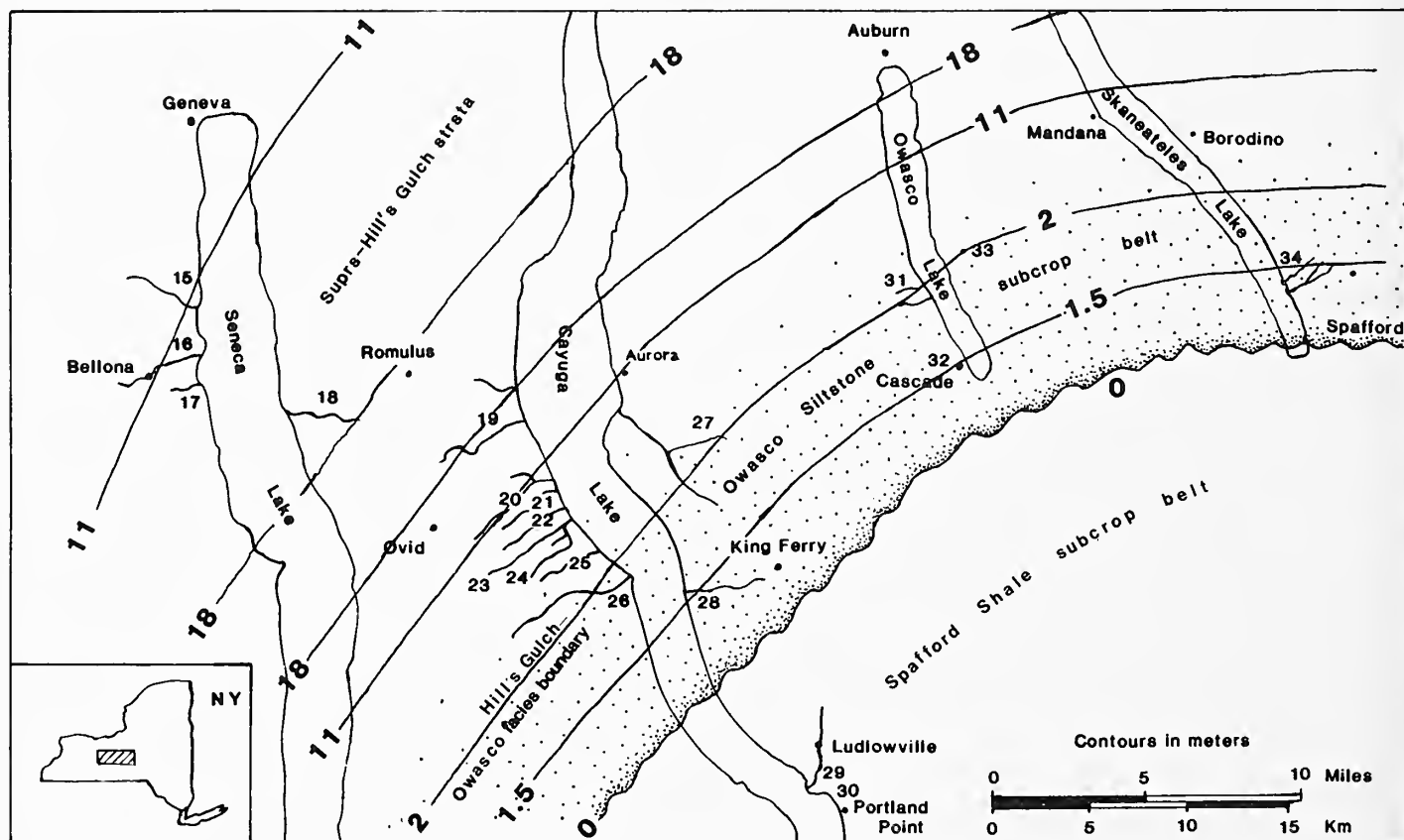


Figure 14. Sub-crop map of strata beneath Tichenor Limestone basal unconformity. Isopachs show prominent southeastward beveling of Jaycox beds under the Tichenor Limestone. Post-Hill's Gulch Bed-Owasco Siltstone (middle-upper Jaycox strata) are missing at, and southeast of, the two-meter isopach as a result of sub-Tichenor beveling. The zero isopach marks the southeastward erosional limit of lower Jaycox-equivalent deposits (Owasco Siltstone). The stippled belt denotes the distribution of silty, condensed lower Jaycox deposits (Owasco Siltstone) within the study area.

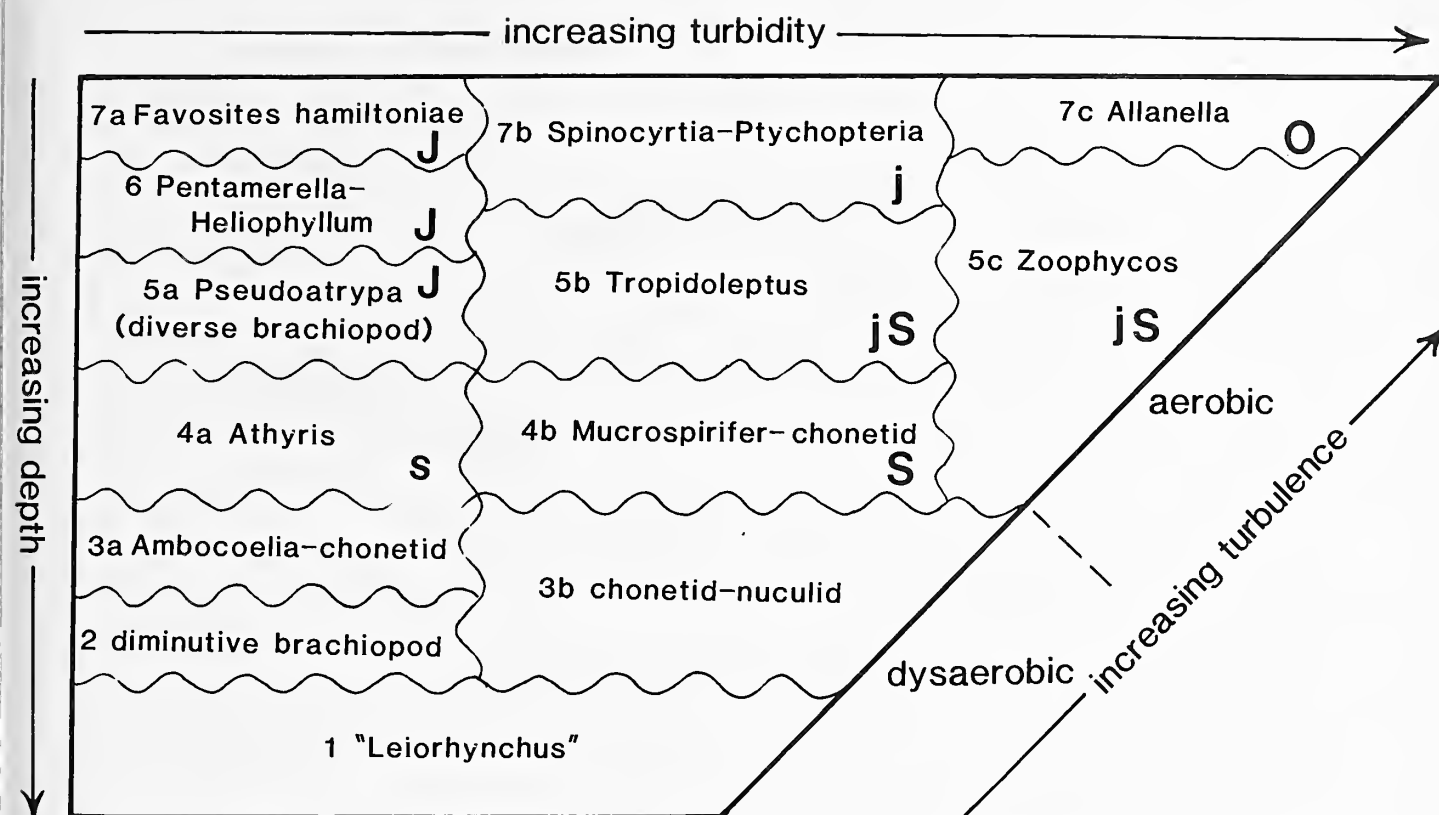


Figure 15. Paleoeological model relating Ludlowville biofacies to inferred bathymetry, sediment accumulation rate, and turbidity. Biofacies of western Jaycox Member marked with "J," those in central trough facies with "j," those in Spafford Member with "S," and those from Owasco Siltstone with "O." Adapted from Brett et al. (1990).

Tropidoleptus association (Figure 16B), which inhabited a soft substratum and which was often buried during episodes of bottom "smothering" (obration). The Limerick Road Bed and parts of the Benton Run Mudstone interval yield very sparse, low-diversity faunas of the *Athyris* biofacies unit; this association records very quiet and extremely turbid bottom conditions hostile to most filter-feeding organisms.

In particular, the functional morphology of several key taxa within the *Tropidoleptus* and *Athyris* associations, including the tabulate coral *Pleurodictyum* and the brachiopods *Mucrospirifer*, *Devonochonetes*, *Longispina*, and *Tropidoleptus*, are known to be adapted for soft, unstable bottoms (Figure 16B and D). These forms are analogous to either sessile "icebergs" or "snowshoes" that rested on the water-rich, muddy, bioturbated substrates.

Even more indicative of obrution conditions are "barren" mudstone intervals that yield extremely few shelly taxa. Most notable within the lower Jaycox Member is the "barren" interval that yields the soft-bodied, problematical discoidal fossils discussed above (Figure 10C). Although this may be a Jaycox biofacies distinct from all others, it is tentatively grouped close to the *Mucrospirifer*-*chonetid* association (Figure 15), because *Mucrospirifer* and *Devonochonetes* are occasionally found associated with the "disks." This association records very quiet and extremely turbid conditions at or near storm wavebase. As discussed below, the *Tropidoleptus* and *Mucrospirifer*-*chonetid* biofacies units are closely associated with the subsiding Romulus Sag.

In central New York, paleosettings of the Jaycox Member are characterized by siliciclastic silt and fine sand substrates, and include two additional biofacies units (Figure 16D and F). The first is the *Zoophycos*

association, which is dominated by the fodinichnial taxon *Zoophycos* and is present in silty mudstone to muddy siltstone deposits of the Jaycox Member (Figure 16D). Sediment churning and undercutting by the deposit-feeding, *Zoophycos*-producing animal is believed to have rendered the sea floor too unstable for habitation by most filter-feeding benthos (see Rhoads, 1974, for discussion). Thus this condition of bioturbation-induced trophic group amensalism resulted in a low-diversity and low-density fauna in this biofacies. The second is the *Allanella* biofacies association, which is associated with Jaycox-equivalent fine sand deposits (Owasco Siltstone) in central New York (Figure 16F). Although this sandy substratum was generally firmer than that of the *Zoophycos* association, the tendency for the sand to shift during storms resulted in an environmental setting that was unsuitable for all but a few hardy, opportunistic filter-feeding taxa.

Jaycox biofacies: western New York

In the thin, condensed packstone facies in Erie and Genesee Counties, the Hill's Gulch Bed has coral-rich associations that are typical of the medium-high-energy, more mud-starved deposits of the *Favosites hamiltoniae* biofacies association. The Hill's Gulch Bed ramps eastward (basinward) through a more silt-influenced "hybrid" *Pentamerella-Heliophyllum-Tropidoleptus* biofacies in the Hill's Gulch-Genesee Valley region, and then into a *Tropidoleptus* biofacies in the Honeoye Valley-Seneca Lake region. The Demosponge-*Megastrophia* bed similarly undergoes an eastward facies change from a diverse brachiopod biofacies at its western extremity to the "*Tropidoleptus*" biofacies in the Seneca Lake Valley. Both the Green's

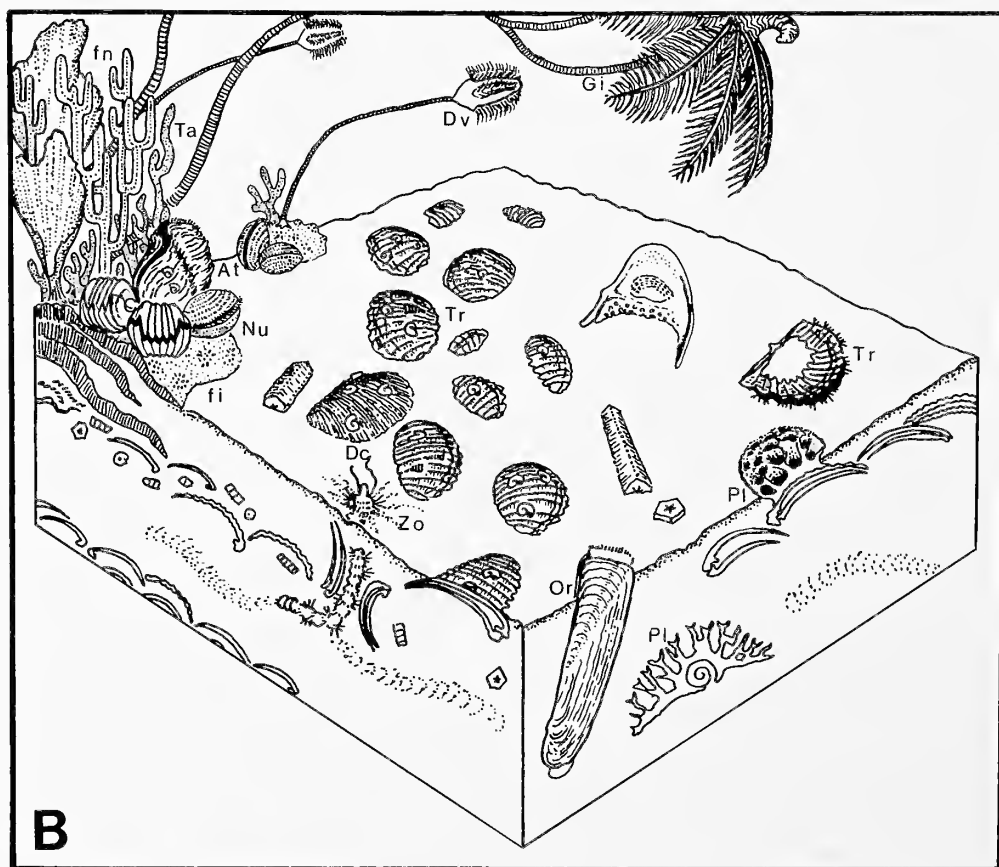
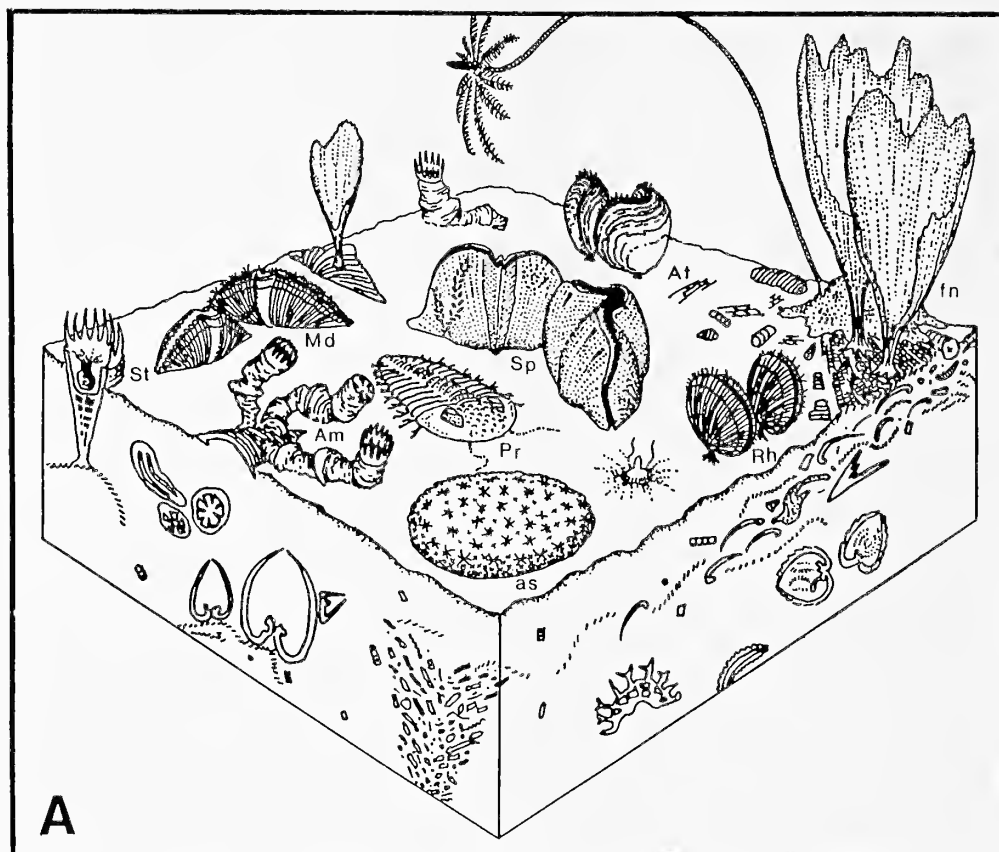


Figure 16 A, B. Intermediate depth, fully aerobic environments of the uppermost Ludlowville Formation. Distinct biofacies developed at similar depth ranges under varying conditions of turbidity/sediment accumulation rate and substrate consistency. *A*, Diverse brachiopod biofacies representing low turbidity/sediment accumulation rate and shelly mud substrate conditions. At, *Athyris spiriferoides*; Md, *Mediospirifer audaculus*; Rh, *Rhipidomella vanuxemi*; Sp, *Spinocyrtia granulosa*; Am, *Amplexiphyllum hamiltoniae*; St, *Stereolasma rectum*; as, astreosponge; fn, fenestellid bryozoan; Pr, *Phacops rana*. *B*, *Tropidoleptus* biofacies representing intermediate to high turbidity/sediment accumulation rate and silty mud substrate conditions. At, *Athyris spiriferoides*; C, *Cupulorostrum* sp.; Dc, *Devonochonetes coronatus*; Nu, *Nucleospira concinna*; Tr, *Tropidoleptus carinatus*; Pl, *Pleurodictyum americanum*; Or, *Orthonota undulata*; Gi, *Gilbertocrinus*; Dv, *Devonoblastus leda*; fi, fistuliporoid bryozoan; Ta, *Taeniopora exigua*; Zo, *Zoophycos*.

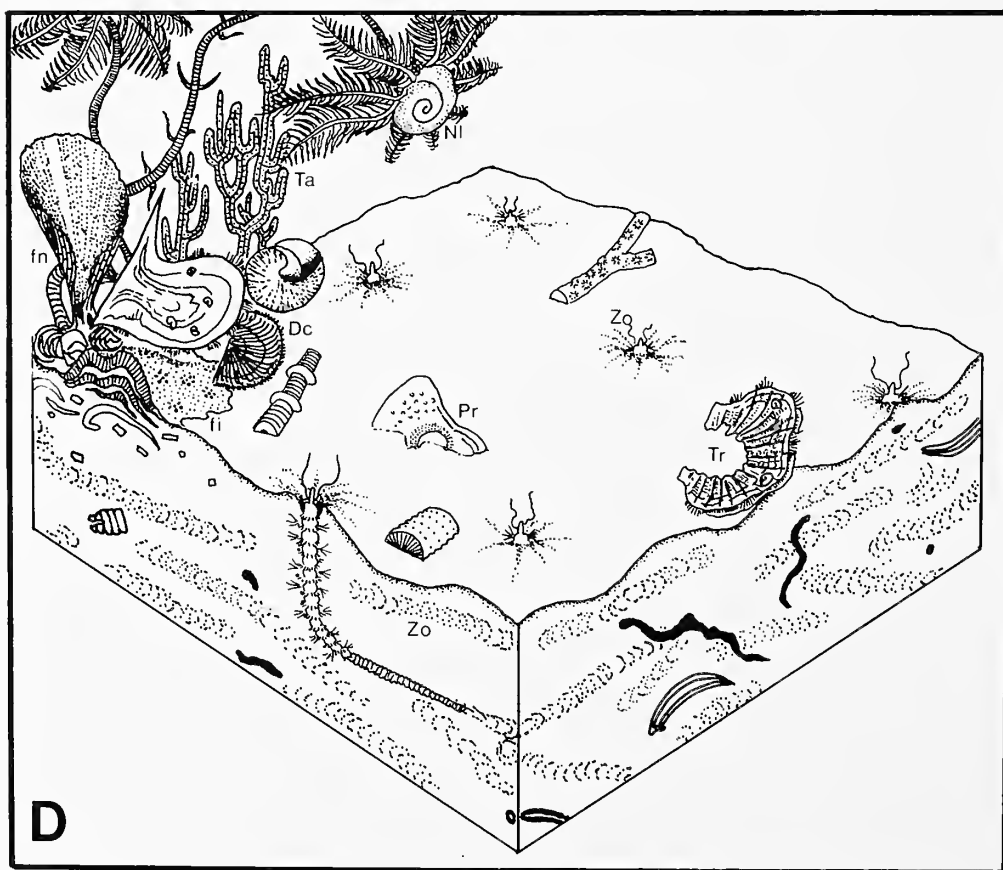
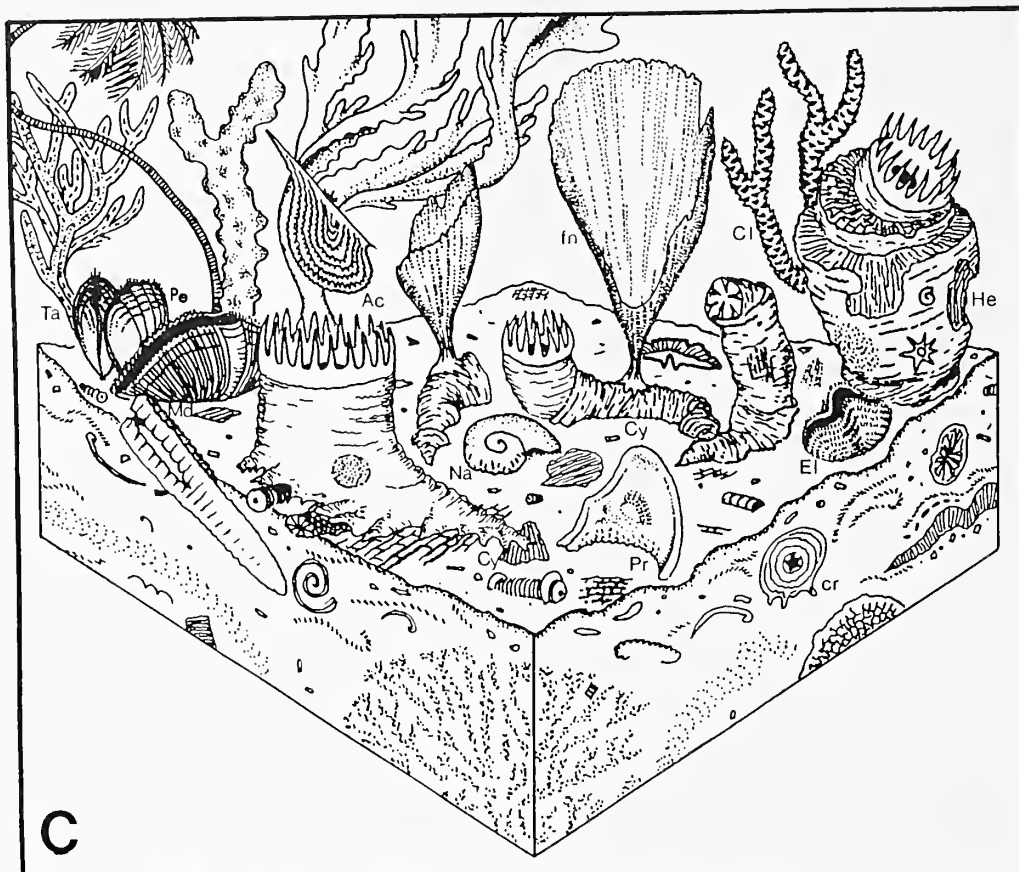


Figure 16 C, D. Moderately shallow, fully aerobic environments of uppermost Ludlowville Formation. Two different biofacies developed under differing conditions of turbidity/sediment accumulation rate. C, *Pentamerella–Heliophyllum* biofacies representing low turbidity/sediment accumulation rate and shelly mud substrate. E, *Elita fimbriata*; Md, *Mediospirifer audaculus*; Pe, *Pentamerella pavillionensis*; ds, demosponge; Cl, *Cladopora?* sp.; Cy, *Cystiphyllodes* spp.; He, *Heliophyllum halli*; Ac, *Actinopteria decussata*; Na, *Naticonema lineatum*; cr, *in situ*, reptate camerate crinoid stem; fn, fenestellid bryozoan; Ta, *Taenipora exigua*; Pr, *Phacops rana*. D, *Zoophycos* biofacies representing intermediate to high turbidity/sediment accumulation rate and silty substrate. Dc, *Devonochonetes coronatus*; fn, fenestellid bryozoan; fi, fistuliporoid bryozoan; Ta, *Taenipora exigua*; Li, *Leiopteria* sp.; Na, *Naticonema lineatum*; Pr, *Phacops rana*; Zo, *Zoophycos*. From Brett et al. (1990).

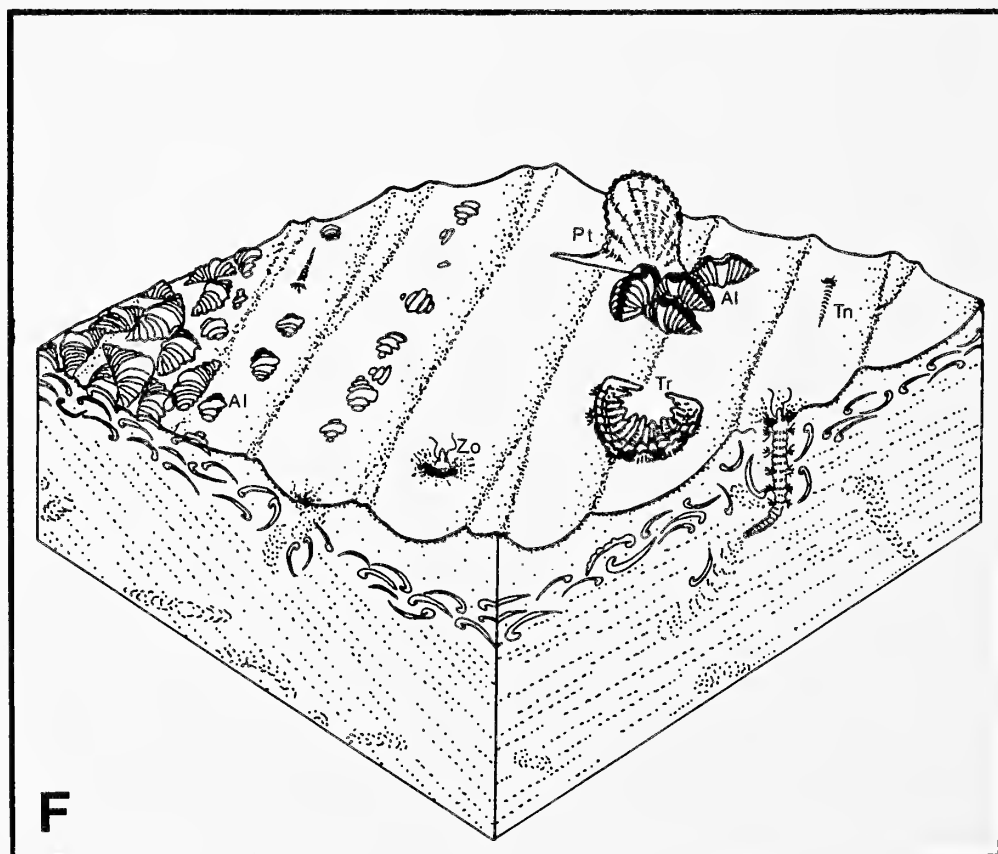
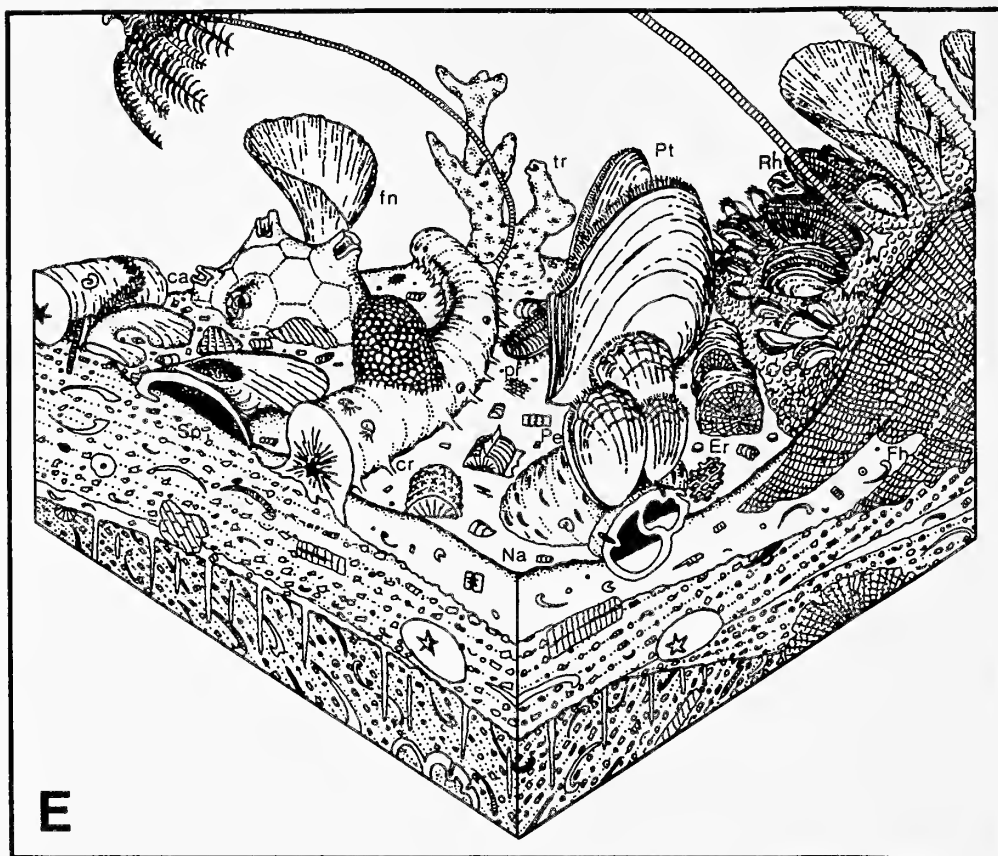


Figure 16 E, F. Shallow, near-normal wavebase environments of uppermost Ludlowville Formation. Two distinct biofacies developed under differing conditions of turbidity/sediment accumulation rate or substrate consistency. *E*, *Favosites hamiltoniae* biofacies representing low turbidity/sediment accumulation rate conditions and a skeletal sand substrate. Note cross-stratified skeletal debris in upper portion of sediment cross-section and bored hardground in lower; also note worn brachiopod valves at sediment surface. *Er*, *Eridophyllum subcaespitosum*; *Fh*, *Favosites hamiltoniae*; *Ce*, *Centronella impressa*; *Me*, *Meristella* sp.; *Pe*, *Pentamerella pavillionensis*; *Rh*, *Rhipidomella* sp.; *Sp*, *Spinocyrtia granulosa* (worn valve); *Pt*, *Plethomytilus oviformis*; *Na*, *Naticonema lineatum*, note barnacle borings in shell; *fn*, fenestellid bryozoan; *tr*, trepostome bryozoan; *pr*, proetid trilobites; *cr*, crinoid runner; *ca*, large calyx of camerate crinoid. *F*, *Allanella* biofacies representing intermediate to high turbidity conditions and a fine sandy substrate. *Al*, *Allanella tullius*; *Tr*, *Tropidoleptus carinatus*; *Pt*, *Ptychopteria fabellum*; *Te*, *Tentaculites*; *Zo*, *Zoophycos*. From Brett et al. (1990).

Landing and the Cottage City Coral Beds change eastward (and down-gradient) from the muddier, lower-energy *Pentamerella*–*Heliophyllum* biofacies in western New York into a lower-energy, diverse brachiopod biofacies in Seneca Lake valley localities (Figure 15).

Jaycox biofacies: Seneca Valley–Skaneateles Valley region

From Sampson State Park to Mack Creek, almost all of the Jaycox Member is dominated by the *Tropidoleptus* and *Mucrospirifer*–chonetid biofacies associations (Figure 15), although many mudstone intervals in this region contain too few fossils for adequate biofacies characterization. The Limerick Road Bed grades eastward from the *Athyris* biofacies in western localities to the *Tropidoleptus* biofacies in central New York. The “barren” shale displays the *Mucrospirifer*–chonetid biofacies association, and the *Tropidoleptus* biofacies association (*Tropidoleptus*, *Grammysia*, *Pleurodictyum*, *Cypricardella*, *Zoophycos*) is exhibited in the Hill’s Gulch interval.

Southeast of Mack Creek, the Limerick Road Bed becomes difficult to recognize, but the Limerick Road Bed and the lower Jaycox “barren” mudstone interval both grade southeastward into the Spafford Member. Southeast of Mack Creek to the vicinity of King Ferry, the lower part of this “barren” interval displays the *Mucrospirifer*–chonetid biofacies association, and the upper part, below the Owasco Siltstone, has a *Tropidoleptus* biofacies. Still farther to the east and south, the “barren” interval thickens into facies more typical of the Spafford Member. The lower 2.0 to 3.0 m of this unit has a “hybrid” *Tropidoleptus*–*Pseudoatrypa*-rich diverse brachiopod assemblage, the medial 2.0 to 3.0 m has the *Tropidoleptus* biofacies, and the upper 2.0 to 3.0 m is referable to the *Zoophycos* biofacies association (Figure 14). Near Lansing, Tompkins County, and at Cascade, the lower Spafford Member has

blue-grey mudstones that contain the tabulate coral *Pleurodictyum*; the brachiopods *Mucrospirifer*, *Pseudoatrypa*, *Longispina*, *Schuchertella*, *Spinocyrtia*, and *Tropidoleptus*; the bryozoan *Sulcoreteopora*; and the bivalves *Grammysia*, *Orthonota*, and *Modiomorpha*. Overlying middle Spafford silty mudstone beds contain *Tropidoleptus*, *Mucrospirifer*, *Grammysia*, *Modiomorpha*, and abundant *Zoophycos*. The silty uppermost Spafford Member contains abundant *Zoophycos* with *Tropidoleptus*, *Mucrospirifer*, and numerous pteroid and modiomorphid bivalves. This vertical succession persists eastwards to Syracuse (Smith, 1935; Muscatt, 1967; Grasso, 1970).

As the Hill’s Gulch Bed of the Seneca Valley is traced east-south-eastward into the Owasco Siltstone of the southern Cayuga, Owasco, and Skaneateles Valleys, it changes from a *Tropidoleptus* biofacies in the Kashong Glen–Mack Creek region, through a *Zoophycos* biofacies association in the Barnum Creek area, into an *Allanella* biofacies at Sheldrake Creek and at sections east of there (Figure 17). In the Kashong–Mack Creek area, this interval contains abundant *Tropidoleptus*. Southeastward, it contains abundant *Zoophycos* and body fossils, including *Tropidoleptus*, pteroid bivalves, and the trilobite *Dipleura*. Still farther east, cross-laminated deposits of the Owasco Siltstone *sensu stricto* contain a low-diversity association of abundant *Allanella* with fewer *Tropidoleptus*, pteroid bivalves, and *Zoophycos*.

Above the Hill’s Gulch Bed, the persistent *Tropidoleptus*–*Longispina* interval corresponds to the *Tropidoleptus* biofacies association. Between Jaycox Creek and Kashong Glen, the coral–brachiopod-rich *Pentamerella*–*Heliophyllum* biofacies generally changes eastward into the diverse brachiopod association. Only 2.0 to 3.0 m of coral–shell bed-equivalent diverse brachiopod biofacies is observed at Kashong Glen in a 15 m-thick section (Figure 9). As indicated above, this

BIOFACIES GRADIENT MAP FOR HILL’S GULCH–OWASCO TIME

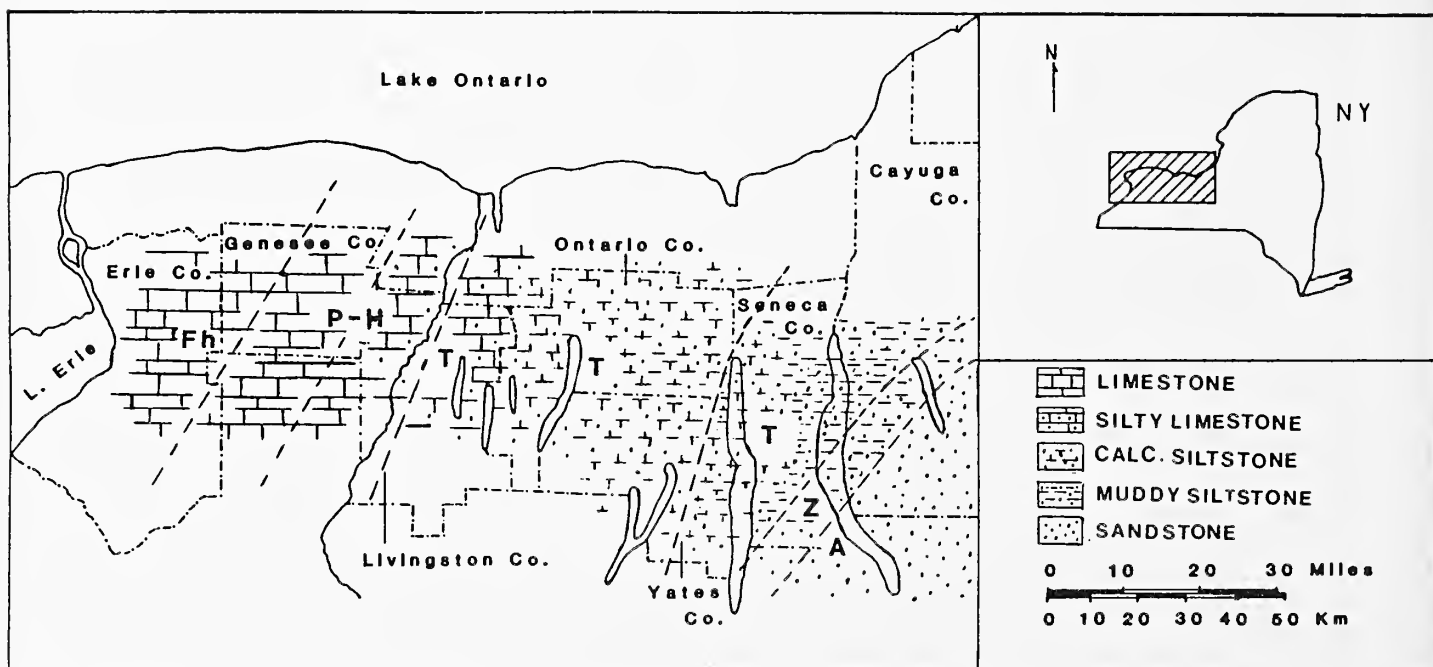


Figure 17. Litho- and biofacies distribution of the lower Jaycox Member. Figure shows an approximate time transect of the Hill’s Gulch Bed–Owasco Siltstone. Abbreviations for biofacies include FH, *Favosites hamiltoniae*; PH, *Pentamerella*–*Heliophyllum*; T, *Tropidoleptus*; Z, *Zoophycos*; A, *Allanella*; see Figure 16 for illustrations of these biofacies. Inset map shows location of study area.

sequence is largely correlative with the Green's Landing Coral Bed–Cottage City Coral Beds interval farther west, and it can be traced at least as far east as Sampson State Park. East of that locality, this facies is absent, except for the problematical thin coral-rich bed immediately beneath the Tichenor Limestone at Mack Creek. Most of the Benton Run Mudstone between Canandaigua Lake and Sampson State Park is composed of a combination of mudstone with *Tropidoleptus* associations and siltstone beds that represent a *Zoophycos* biofacies. These beds contain abundant *Zoophycos* and pteroid bivalves with local patches of *Sulcoretepora* and pelmatozoan debris. The problematic siltstone interval that composes the highest exposed strata of the Jaycox Member at Big Hollow Creek has a *Zoophycos* association. If this unit is part of the Benton Run Mudstone, then it presumably grades westward into a *Tropidoleptus* biofacies that corresponds to the typical Benton Run Mudstone at Kashong Glen. Although there are apparent rapid southeastward (shoreward) biofacies changes above the Hill's Gulch Bed of the Jaycox Member from Sampson State Park across the Cayuga Valley, too much of the middle and upper Jaycox Member has been removed by submarine erosion to provide a complete biofacies spectrum for Jaycox beds on the southeast margin of the Romulus Sag.

Stratigraphic trends and facies gradients of the Jaycox Member

Jaycox stratigraphic trends: western New York

The Jaycox Member thickens notably eastward towards the Romulus Sag, a region of contemporaneous differential subsidence and terrigenous sediment accumulation in the Seneca–Cayuga Valley area that strongly influenced depositional patterns through much of the Givetian. The Jaycox Member thickens eastward across Genesee, Livingston, and Ontario Counties in a seemingly exponential pattern. However, only minor thickening takes place west of the Genesee Valley, with a more substantial expansion from the Genesee Valley into the Canandaigua Valley, and relative ballooning of the aggregate section in the Seneca Lake Valley (Figures 9, 13, and 14). This mirrors the exponential eastward thickening of the Deep Run Member of the lower part of the overlying Moscow Formation in the Canandaigua Lake region (see Baird, 1979; Baird and Brett, 1981).

This eastward stratigraphic trend is also mirrored by biofacies gradients. Most units of the Jaycox Member show an eastward trend from a high-diversity biofacies dominated by epifaunal filter-feeding organisms (*Favosites hamiltoniae*, *Pentamerella–Heliophyllum*, and diverse brachiopod associations) to lower-diversity associations of opportunistic taxa (*Tropidoleptus* and *Mucrospirifer*–chonetid biofacies) that could tolerate higher turbidity, soft substrates, and higher sediment accumulation rates (Brett et al., 1986; Vogel et al., 1987). The *Favosites hamiltoniae* biofacies in western sections grades eastward and downslope into a *Pentamerella–Heliophyllum* and then a diverse brachiopod or *Tropidoleptus* biofacies. Similarly, the *Tropidoleptus* and/or *Mucrospirifer*–chonetid biofacies grade eastward into barren or sparsely fossiliferous, *Zoophycos*-bioturbated deposits within the central Finger Lakes depocenter.

A large part of the rapid southeastward thickening of the Jaycox Member into the Seneca Lake Valley may simply be due to the eastward appearance of the Benton Run Mudstone beneath the sub-Tichenor disconformity. The reduction in apparent duration of the sub-Tichenor hiatus is consistent with Jaycox thickness and biofacies trends that are indicative of differential subsidence in the central Finger Lakes

region. However, thickness trends for individual units from the Green's Landing Coral Bed upwards to the Cottage City Coral Beds are less clear-cut; most of these units thicken eastward into the Canandaigua Valley, but they apparently thin again towards Seneca Lake (Figure 9). Moreover, there are major thickness changes for these beds between adjacent sections in the Canandaigua Valley that suggest that local depositional controls may have been important in the deposition of coral- and shell-rich biofacies (see Mayer, 1989).

Relationship of stratigraphic and biofacies trends to Romulus Sag

Stratigraphic patterns and biofacies trends within the Jaycox Member across western and central New York closely mirror those for subjacent and superjacent divisions (see Figure 2 for terminology), particularly for the overlying Tichenor Limestone and Deep Run Member of the Moscow Formation. As with the Tichenor–Deep Run interval, the Jaycox Member of western New York is thin, carbonate-rich, and condensed, and thickens only gradually eastward to the vicinity of the Genesee Valley. East of the Genesee Valley, the Jaycox Member thickens more rapidly to the vicinity of the Canandaigua Valley and becomes progressively more dominated locally by a sparsely fossiliferous mudstone facies. This latter lithology is characteristic of the greatly expanded Deep Run section in the same area.

East of the Canandaigua Valley, the Spafford Member begins to balloon into a sparsely fossiliferous mudstone sequence in the Seneca Valley–northern Cayuga Valley region (Figure 6). This region also coincides with the most prominently developed, dysoxic, dark grey mudstone biofacies of the underlying Wanakah Member (Baird and Brett, 1981; Brett et al., 1986), as well as with the maximum observed thickness of unbeveled Benton Run Mudstone and the thickest and most argillaceous facies of the Tichenor Limestone. Southeast of this persistent depocenter, the Jaycox Member rapidly thins and coarsens as a result of stratigraphic condensation and erosional overstep, a pattern that areally corresponds to the southeastward condensation and biofacies change within the lower Wanakah Member (Miller et al., 1988; Brett et al., 1986), the Tichenor–Menteth interval, and the still higher Kashong Member (Baird, 1979; Baird and Brett, 1981).

One particular taphonomic signature of the axis of the Romulus Sag is the local abundance of the compressed, discoidal, soft-bodied organisms of the Spafford Member between Seneca and Cayuga Lakes. These fossils display the best preservation and occur in the thickest stratigraphic interval in the Sheldrake–Big Hollow Creek area, but show a dramatic reduction in preservation quality and vertical distribution to the east and southeast of King Ferry and to the west of Seneca Lake. Because rapid burial events apparently explain the occurrence of these forms, the westward disappearance of this taxon within the Spafford Member mudstones can be correlated with westward thinning of that unit and lower implied sediment accumulation rates. The eastward disappearance of the disks within the silty, bioturbated facies of the upper Spafford Member can also be attributed to slower accumulation rates and the consequent effects of aerobic decay and scavenging.

Biofacies gradients east and west of the Romulus Sag mirror the stratigraphic patterns, although the biofacies are fundamentally different on opposite sides of the depocenter (Figure 17). A complete biofacies spectrum can be observed only for the lower Jaycox Member (Hill's Gulch Bed) because of pinchout and/or erosion of higher units at the basin margins. To the west is the upslope gradient from mud- and turbidite-dominated facies in the central Finger Lakes region to relatively sediment-starved, higher-energy, firm-bottom conditions that supported

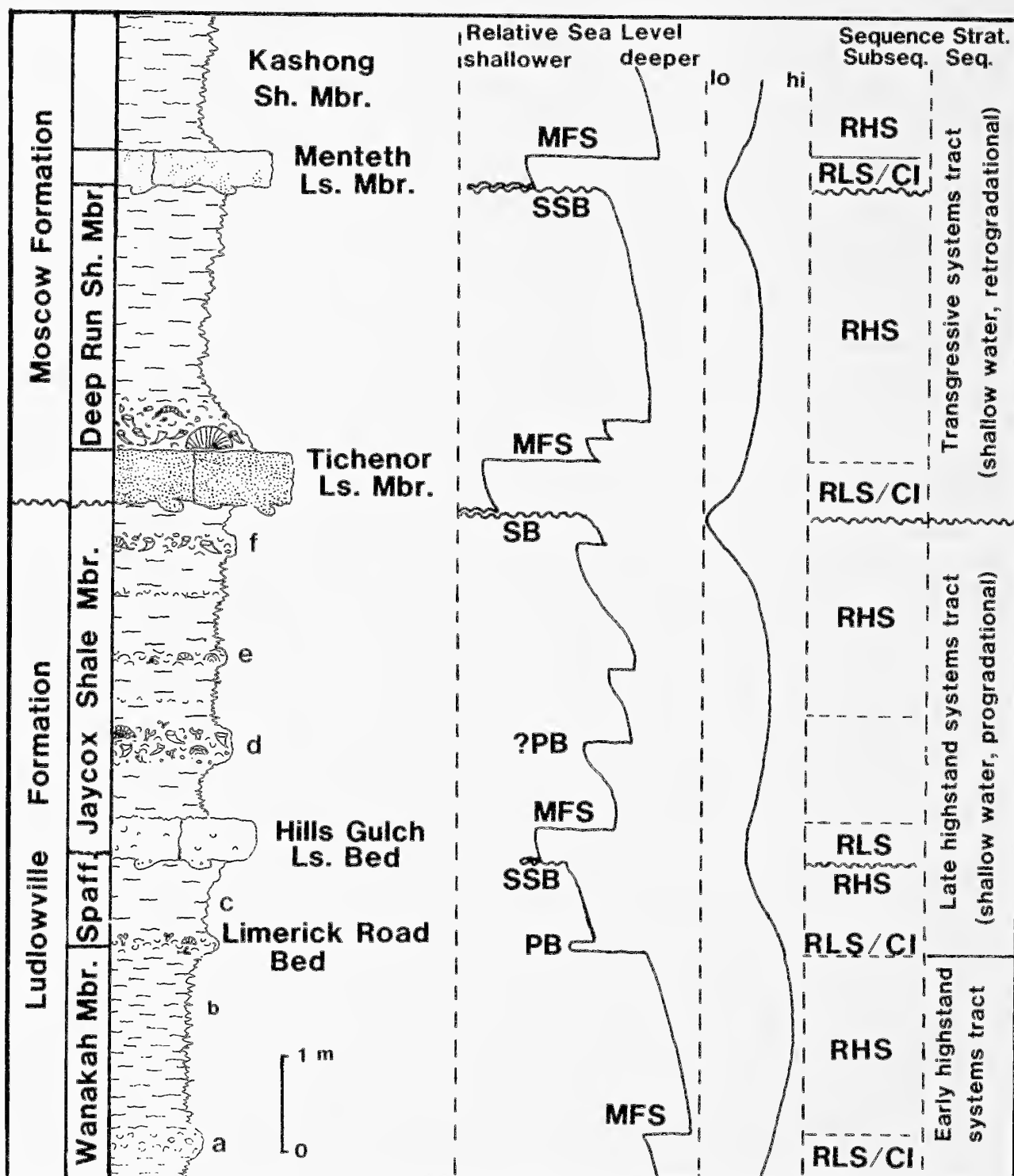


Figure 18. Sequence stratigraphy model applied to a portion of the upper Hamilton Group. Deposition of upper Ludlowville Formation divisions (uppermost Wanakah Member and Jaycox Member) and lower Moscow units (Tichenor Limestone and Deep Run, Menteth, and basal Kashong Members) is shown to be influenced by rises and falls of sea level. Major regressive event at base of Moscow Formation (discontinuity under Tichenor Limestone) is traceable across most of New York State and probably marks a sequence boundary (SB). Other discontinuities (underneath Hill's Gulch Bed and Menteth Limestone) mark subsequence boundaries (SSB). PB=Precursor Beds (see text). Remaining terms include MFS=Marine Flooding Surface, RHS=Relative Highstand, RLS=Relative Lowstand, CI=Condensed Interval. Units include (a) Bloomer Creek Bed; (b) upper Wanakah mudstone with diminutive dysaerobic fauna; (c) barren, blocky mudstone unit; (d) Green's Landing Coral Bed. Modified from Brett and Baird (1990).

diverse coral associations (*Heliophyllum*, *Favosites hamiltoniae*; Figure 17). To the east-southeast of the Romulus Sag axis, however, is an up-slope change from the mud- and turbidite-dominated depocenter to a moderately turbid but current-winnowed shelf setting characterized by silt and sand substrates. This is particularly well-displayed along the Hill's Gulch Bed–Owasco Siltstone transition by the rapid southeastward biofacies gradient from a *Tropidoleptus* biofacies in the Seneca–northern Cayuga Valley region, to a *Zoophycos* biofacies southeast of the depocenter axis, and finally to an *Allanella* biofacies east of the Cayuga Valley (Figure 17). Although depositional environments again become shallow southeast of the Romulus Sag, there is not a return to diverse, firm-bottom, clear-water biofacies comparable to those on the platform northwest of the trough. The absence of corals, diverse brachiopods, and bryozoans within the coarse siltstone to fine sandstone of the Owasco Siltstone points to turbid, unstable-bottom, higher-energy conditions that excluded all but a few opportunistic forms.

The Owasco shelf is a prime example of a sediment-bypass facies that results from sediment-aggradation rate exceeding accommodation space for its accumulation and producing a thin “condensed” sandstone deposit. This differs fundamentally from the sediment-starved, carbonate- and shell-rich condensed facies of the western Jaycox Member, which are distinguishable from those of the Owasco Siltstone by their lithology and fauna. Sediment-starved sequences can be distinguished from sediment-bypass facies by means of the architecture of component sedimentary cycles (see below).

This pattern confirms the presence of an active belt of differential subsidence and sedimentary accumulation that obliquely crossed the subtidal Jaycox shelf in the Seneca and northern Cayuga Valley region. Although this northeast-southwest-trending depocenter is recognized in underlying units of the Ludlowville Formation (Baird, 1981; Gray, 1984; Brett et al., 1986; Miller et al., 1988) and overlying lower members of the Moscow Formation (Baird, 1979; Baird and Brett, 1981), earlier correlations of the Jaycox Member were too sketchy to identify such patterns with certainty. This stratigraphic report shows that the Romulus Sag was an active feature coincident with Jaycox deposition, and that it affected thickness trends, biofacies gradients, and the extent and magnitude of discontinuities.

Cyclic and sequence interpretation of the Jaycox Member

The Middle Devonian section in New York State contains numerous thin lithostratigraphic units and fossil-rich layers (epiboles) with unique taxonomic composition and/or taphonomic character that can be traced across magnafacies belts for great distances (Brett et al., 1986, 1990). Numerous beds, zones, and sedimentary cycles within the Ludlowville and Moscow Formations appear to record isochronous depositional events. A critical first test to determine whether a bed or sedimentary cycle is of circumbasinal or extrabasinal extent is to determine whether its signature can be mapped across facies strike so as to provide an event link between strongly contrasting facies. The Spafford–Jaycox interval provides an opportunity to assess the spatial-temporal character of component units by determining which units can be mapped across the facies spectrum of the Romulus Sag.

Thin, distinctive beds traceable across the western New York shelf include the Limerick Road Bed, the Hill's Gulch Bed, the Green's Landing Coral Bed, and the Cottage City Coral Beds. The

thin character of these units, and their tendency to thicken slightly and to show an internal gradation of biofacies towards the eastern depocenter, is consistent with the isochronous interpretation of these layers (Mayer et al., 1990; this report). The fact that the Hill's Gulch Bed can be correlated across the Finger Lakes into the Owasco Siltstone strongly indicates that this unit records a widespread shoaling event of probable allocyclic (extrabasinal) extent (Figure 18). It is suspected that both the Green's Landing Coral Bed and the Cottage City Coral Beds were the products of widespread events, but the southeastward and westward truncation of both units by the sub-Tichenor disconformity prevents lateral tracing of these beds. Jaycox units of lesser areal extent, including the zone of soft-bodied discoidal fossils in the lower Jaycox Member, the Demosponge–*Megastrophia* bed, and the interval of large *Pleurodictyum* in the lower Benton Run Mudstone west of Seneca Lake, may have been as extensive as the four units enumerated above. However, the varied effects of taphonomic and paleoenvironmental gradients, plus overstep by the Tichenor Limestone, makes these units difficult, if not impossible, to trace over large distances.

The widespread character of several Spafford–Jaycox subdivisions (Limerick Road Bed, Hill's Gulch Bed, Green's Landing Coral Bed, Demosponge–*Megastrophia* bed, Cottage City Coral Beds) indicates that they are not the result of short-term events, such as storms or single colonization events, but are multi-event units that record changes in sea level and climate. The fact that the Hill's Gulch Bed grades eastward into a cross-laminated sandstone suggests that this unit records a regression event; particularly convincing is the upward-coarsening motif of the Spafford Member below the Owasco Siltstone cap (Figures 13 and 18).

Similarly, the dramatic upward change from the dysoxic upper Wanakah Member, with a diminutive brachiopod facies, into the shelly, silty grey debris layer of the Limerick Road Bed suggests that this basal Spafford unit also marks a shallowing event. However, this shallowing episode was only an initial phase of a sea-level drop that culminates in the Hill's Gulch–Owasco shoaling event. In addition, there appears to be no upward regressive hemicycle motif that culminates in the Limerick Road Bed. In fact, the Limerick Road Bed is coincident with an erosional, diastemic surface on the dark shales of the upper Wanakah Member. All the more significant is the association of this hiatus with the axial region of the subsiding Finger Lakes area, and also with the occurrence of abundant enigmatic discoidal fossils in the superjacent “barren” mudstone beds. Moreover, the Limerick Road Bed appears to amalgamate eastward with the Bloomer Creek Bed of the underlying Wanakah Member southeast of Mack Creek, just where the Hill's Gulch Bed begins to transform from a more basinal facies into a regressive, hemicycle-capping siltstone.

This type of bed has been observed at five other levels within the Hamilton Group in nearly identical stratigraphic contexts. Because such beds appear as abrupt bases to regressive shoaling cycles and display faunal and lithologic features normally associated with the regressive peak, they have been termed “precursor beds” (Brett et al., 1990). These units are not fully understood in terms of existing depositional models, but they appear to mark the onset of important processes at the beginning of regression within foreland basins. In the context of sequence stratigraphy, such beds are neither sequence boundaries nor maximum flooding surfaces, although they share some features with the latter. Rather, they appear to occur at the boundary between early and late highstand (i.e., between deep-water aggradational and upward-shallowing progradational depositional phases). They may represent the caps of very minor PAC-scale cycles, or a type of con-

densified deposit that reflects sediment starvation during early phases of sea-level fall. One possibility is that when streams adjust to a lower base level, they may deposit a considerable amount of sediment within these valleys and thereby cause a brief interval of offshore sediment starvation during early regressive phases before sediment progrades seaward (Posamentier et al., 1988; Posamentier and Vail, 1988). It is possible that they are a small-scale analog of a sequence boundary deposit, where an unconformity is directly overlain by sediment-starved transgressive deposits associated with rapid sea-level drop and rapid seaward sediment migration. The Limerick Road Bed and other "precursor beds" may be as important as the widely recognized regressive half-cycles in the interpretation of foreland basin cyclic sedimentation.

In contrast to the Limerick Road and Hill's Gulch Beds, the diverse coral-brachiopod beds appear to record minimal sediment accumulation rates punctuated by rapid, storm-induced mud accumulation. These beds may cap minor shallowing cycles and/or be associated with ensuing transgression events or concurrent climatic change. Initial transgressive migration of the strandline away from the western New York shelf would have resulted in reduced turbidity. This, in turn, would have allowed more shelly, filter-feeding taxa to colonize the bottom. A consequent development would have been production of a more stable substrate with a shelly pavement that allowed colonization by the abundant and diverse assemblages characteristic of the coral beds in western New York (see Mayer, 1989).

The sub-Tichenor disconformity records a major regression that terminates deposition of the Ludlowville Formation (Figure 18). The blanket of Tichenor packstone-grainstone encrinite records the first deposition of Moscow Formation sediments during a succeeding transgressive event (Baird and Brett, 1981; Brett et al., 1986); this pelmatozoan-shell-coral debris sheet records initial deposition following the high-energy erosive regression maxima and probable depths within fair-weather wavebase. The Tichenor encrinite grades upward through interbedded storm layers, bryozoan-crinoid "lettuce-stone" buildup, and obrution mudstone bands of the lower Deep Run Member into the dominantly poorly fossiliferous mudstone of the higher Deep Run. This overall succession is transgressive in character and largely mirrors the regressive upper Jaycox to sub-Tichenor disconformity succession (Brett et al., 1986).

Thus the Spafford-Jaycox interval constitutes the lower half of a large-scale regressive-transgressive couplet ("Tichenor Cycle"), one of approximately four similar cycles in the Hamilton Group. The Jaycox-Tichenor-Deep Run cycle would best correspond in magnitude to a "fourth-order" cycle (Busch and Rollins, 1984; Johnson et al., 1985). The best-studied Hamilton cycle, the Centerfield regressive-transgressive cycle, is of similar magnitude and has a comparable lithologic succession (see Gray, 1984, 1991; Savarese et al., 1986), but it lacks a major erosional discontinuity at its regressive maximum in New York. The Tichenor cycle appears to record a more prominent shallowing episode that resulted in partial to complete removal of underlying beds of the Jaycox Member. Only in the Seneca Valley-northern Cayuga Valley region was the Jaycox largely spared erosion as a result of deeper water conditions and greater subsidence rates within the Romulus Sag. However, the correlative Hungry Hollow Formation, in presumably shallower shelf settings of southwestern Ontario, has a sharp disconformable lower contact. This disconformity truncates lower Centerfield-equivalent and upper Levanna-equivalent units, and is thus closely analogous to the sub-Tichenor unconformity (Landing and Brett, 1987).

In the still broader perspective of sequence stratigraphy (see Vail et al., 1977; Van Wagoner et al., 1988), the sub-Centerfield disconformity in Ontario and the sub-Tichenor unconformity in New York appear to represent sequence boundaries. They are lowstand unconformities that separate two sequences. In this sense, the Ludlowville and Moscow Formations are analogous to continental margin sequences recognized by seismic stratigraphers (Brett et al., 1990). Lowstand conditions, which reflect a relatively rapid sea-level drop that exceeds the local subsidence rate, are represented only by the unconformity surfaces themselves. Lowstand deposits per se are absent, and transgressive surfaces are thus amalgamated with the sequence boundary. The overlying crinoidal pack- and grainstone (mid-Centerfield Limestone [or Schaeffer Creek Bed of Gray, 1984] and Tichenor Limestone) represent initial transgressive lags deposited in shallow water. These sheet-like deposits grade upward into fossiliferous mudstones (e.g., Deep Run and Kashong Members of the Moscow Formation) and pelletal silty carbonates (calcisiltites) that display the deepening-upward (retrogradational) pattern characteristic of transgressive systems tracts. A sharp surface marked by phosphatic nodules, presumably a surface of maximum sediment starvation, separates these deposits from deep-water, dark grey to black shales. Examples of other sediment-starved units include the Moonshine Falls phosphate bed of the uppermost Centerfield Member and the upper Kashong phosphate bed below the Windom Shale. Early highstand deposits are represented by the considerable thickness of relatively uniform, grey to black shale facies, whereas later highstand deposits record initial regression but display generally upward-shallowing (progradational) patterns. In this model, the Spafford-Jaycox interval represents the late highstand phase of the Ludlowville depositional sequence. The Limerick Road Bed is a precursor bed that marks the top of Wanakah early highstand conditions. The sub-Tichenor unconformity forms the boundary of the overlying Moscow depositional sequence and is overlain by transgressive (but very shallow water) Tichenor-Deep Run-Kashong deposits (Figure 18).

Although the succession from the upper Spafford Member to the sub-Tichenor disconformity is cumulatively regressive, there are smaller-scale, regressive-transgressive units superimposed on this trend (Figure 18). Thus the Spafford-equivalent "barren" shales and overlying Hill's Gulch Bed interval, as well as the corresponding Spafford-Owasco interval, represent a small-scale (fifth-order) shallowing hemicycle. The corresponding deepening phase of the cycle is recorded in the interval of shales between the Hill's Gulch and middle Jaycox fossil-rich beds. A second, and presumably stronger, fifth-order cycle is recorded by the Benton Run Mudstone through unnamed upper siltstone at Big Hollow Creek, although upper portions of the shallowing half-cycle have been removed beneath the Tichenor. The Spafford and lower Jaycox Members thus include a lower regressive-transgressive half-cycle that is bounded at its top by the middle Jaycox "barren" mudstone interval (or *Tropidoleptus-Longispina* mudstone). Overlying middle and upper Jaycox deposits record a step-wise regression up to the sub-Tichenor disconformity. The alternation of shell-coral beds (Limerick Road, Green's Landing Coral, and Cottage City Coral Beds) with shell-poor mudstones in this interval suggests that small-scale (sixth-order?) regressive-transgressive cycles are superimposed on the larger regressive trend. These remain to be studied in greater detail.

In summary, the subunits of the Jaycox Member can be subdivided on the basis of diastems and minor discontinuities into smaller-scale sequence-like units (Figure 18). These are sharply based intervals that display generally deepening-upward trends, and they are most recognizable at basin margins. Because they are of lesser magnitude than true

depositional sequences (such as the Ludlowville and Moscow Formations), they have been termed "subsequences" (Brett and Baird, 1990; Brett et al., 1990).

Subsequences correspond approximately to members and informal sub-members in lithostratigraphy. For the interval discussed herein, a first subsequence would consist of the interval between the Bloomer Creek Bed of the upper Wanakah Member and the base of the Hill's Gulch Bed, or approximately to the Spafford Member. A second subsequence would encompass the main body of the Jaycox Member from the (locally sharp) base of the Hill's Gulch Bed to the basal Tichenor erosion surface. It is notable that this (or Owasco Siltstone) subsequence is conformable at its base, and nearly so at its top, in the central Finger Lakes trough, but becomes sharply demarcated toward the basin margins. The base of the Hill's Gulch Bed becomes sharp and oversteps underlying units northwestward of the Genesee Valley. Similarly, the base of the correlative Owasco Siltstone is conformable near Big Hollow Creek, but is increasingly sharp and erosional southeast of Bloomer Creek. This pattern matches that of the larger sequence boundaries. In turn, subsequences can be split further into smaller packages (parasequence or parasequence sets) bounded by distinctive marker units, such as the Limerick Road, Green's Landing Coral, and Cottage City Coral Beds.

Basin dynamics in the upper Ludlowville–Moscow interval

Foreland basins do not simply form and fill; they are dynamically reconfigured by tectonic stresses during the filling process (see Quinland and Beaumont, 1983; Ettensohn, 1987). Without correlational information about widespread event-strata and sedimentary cycles, one can only generalize that the Middle and Upper Devonian Catskill Delta prograded westward across New York State. However, detailed correlation of small units within the Hamilton Group has revealed the presence of a pattern of westward migration of structurally defined depocenters that crossed the central-western New York platform (Baird and Brett, 1981; Brett and Baird, 1985, 1986; Brett et al., 1986; Miller et al., 1988).

In particular, correlation of thin marker bed units within the Moscow Formation shows that the Romulus Sag progressively shifted westward from central into western New York during deposition of the Moscow Formation (Baird, 1979; Brett and Baird, 1982, 1986; Brett et al., 1986). For example, the Tichenor–basal Deep Run fossil-rich interval has its greatest thickness and terrigenous mud content in the Seneca Valley, and the overlying Deep Run Member is thickest in the Canandaigua Valley. Subsequently, the lower Kashong Member is thickest west of Canandaigua Lake, and the middle and upper Kashong is thickest in the Genesee Valley. Farther westward shift of the depocenter is indicated by the fact that the lower Windom *Ambocoelia umbonata*-rich mudstone interval is thickest in the Genesee Valley to eastern Erie County region, and the upper Windom is thickest in western Erie County.

This westward shift of depocenter can be extrapolated eastward (and stratigraphically downward) through the upper Ludlowville deposits. Thus the Spafford Member reaches maximum thickness in the central Cayuga Valley, whereas the middle and upper Jaycox Member balloons to maximum thickness between the northern Cayuga Valley and Seneca Lake (Figures 9, 13). In short, the pervasive westward drift of this depocenter is explicitly recorded by the Jaycox Member. It is interest-

ing to speculate that the Spafford Member in central and eastern New York may be a collage of imbricated, overlapping mudstone divisions that become progressively younger toward the west in the same manner that overlapping Jaycox and younger mudstone units record the westward drift of the depocenter.

Conclusions

The Spafford and Jaycox Members record a period of regression at the end of the Ludlowville Formation deposition. This interval contains several widespread event beds that grade eastward from extremely fossiliferous, condensed facies in western New York to condensed siltstone and even sandstone deposits in central New York. This lithologic transition takes place across an intervening depocenter where siliciclastic mud was the dominant sediment. The term "Spafford Member" (Smith, 1935) is expanded in this report to include beds (Limerick Road Bed and "barren" mudstone interval below Hill's Gulch Bed) formerly included in the Wanakah Member. Most of the Jaycox-equivalent beds are overstepped by the sub-Tichenor disconformity in the Cayuga Valley. However, the Hill's Gulch Bed is eastwardly correlative with the Owasco Siltstone in central New York sections, and the "barren" shale between the Limerick Road Bed and Hill's Gulch bed–Owasco Siltstone is correlative with the underlying Spafford Member.

The Spafford–Jaycox interval contains at least five significant, regionally mappable, thin event beds. These include, in ascending order: (1) basal Limerick Road Bed and associated diastem; (2) interval of problematic, discoidal, soft-bodied organisms in the middle Spafford Member; (3) Hill's Gulch Bed; (4) Green's Landing Coral Bed; and (5) Cottage City Coral Beds in the Jaycox Member. With the exception of the zone of discoidal fossils, which is largely restricted to the Seneca–Cayuga County region, these marker units can be traced into western New York, where they become thinner, more calcareous, and richer in fossil content. The units illustrate a classic pattern of westward sedimentary condensation before eventual removal as a result of westward erosional overstep by the sub-Tichenor disconformity.

Similarly, beds of the Jaycox Member become markedly condensed and truncated to the southeast of the northern Cayuga Valley, except that condensed Jaycox-equivalent facies in the Skaneateles, Owasco, and southern Cayuga Valleys consist of silty mudstone, siltstone, and sandstone lithologies. These regional stratigraphic trends reveal a north-east-southwest-trending structural belt of differential subsidence and sediment accumulation (Romulus Sag) that was centered in the Seneca Valley and northern Cayuga Valley region during Spafford–Jaycox deposition.

The Spafford and Jaycox Members comprise the lower regressive half of the fourth-order Tichenor regressive-transgressive cycle that begins with dysoxic mudstone facies of the upper Wanakah Member and culminates with the sub-Tichenor disconformity. The upper half-cycle is represented by lower units of the Moscow Formation (Deep Run, Menteth, and Kashong Members). This succession records stepwise regression from oxygen-deficient outer shelf conditions to a very shallow, high-energy regime with sea floor erosion, probably within reach of the fair-weather wavebase. Superimposed on this overall trend are several apparent sub-cycles, most notably a regression that produced the Hill's Gulch Bed and equivalent Owasco Siltstone. Regional correlation of Spafford–Jaycox event beds reveals a pattern of westward migration of the depocenter of the Romulus Sag during Jaycox deposition; it shows that this basin-shift process, already known to have been

important during the deposition of the Moscow Formation, was clearly taking place during Spafford-Jaycox deposition.

Acknowledgments

T.X. Grasso, E. Landing, and G. McIntosh reviewed the manuscript. W. Taylor, H. Kimble, and L. Stockmaster assisted in report preparation. The Petroleum Research Fund (PRF) of the American Chemical Society and National Science Foundation (grants EAR 8313103 and 8816856) supported this research. The PRF supplied \$1,750 in page charges.

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Appendix I

Locality Register

(All quadrangles 1:24,000)

1. Orchard Park Quadrangle—Cazenovia Creek—low falls 60 m upstream and shale banks downstream from Northrup Road bridge and 0.8 km west of Spring Brook.
2. East Aurora Quadrangle—Buffalo Creek—low falls 15 m upstream and shale banks downstream from Bullis Road bridge 3.2 km west of Marilla.
3. Corfu Quadrangle—Eleven Mile Creek—waterfalls next to U.S. Rte. 20 bridge 2.4 km west of Darien Center.
4. Alexander Quadrangle—Murder Creek—low falls 180 m north of U.S. Rte. 20 overpass in Darien.
5. Alexander Quadrangle—Bowen Creek—low falls and shale banks 45 m north of county road bridge 1.6 km north of U.S. Rte. 20.
6. Batavia South Quadrangle—north-facing roadcut on east-west county road near Bethany Center.
7. Le Roy Quadrangle—Hill's Gulch—waterfalls and adjacent shale banks 360 m south of junction of U.S. Rte. 20 and the former Delaware, Lackawanna, and Western Railroad.
8. Le Roy Quadrangle—Browns Creek—low falls and banks 30-105 m west of bridge on Limerick Road 1.6 km west of York.
9. Genesee Quadrangle—Jaycox Creek (south branch)—three waterfalls in close proximity to one another and adjacent shale banks 3.2 km north-northeast of Genesee and 390 m west of New York Rte. 39.
10. Honeoye Quadrangle—Beebe Creek—cutbanks along creek 2.4 km north of Allens Hill and 5.2 km southeast of West Bloomfield.
11. Canandaigua Lake Quadrangle—bluffs along the west shore of Canandaigua Lake 0.8 km north of Menteth Point.
12. Canandaigua Lake—Rushville Quadrangles—Deep Run—two waterfalls and adjacent shale banks on main stream and one waterfall and adjacent shale banks on side tributary 0.8 km north of Cottage City.
13. Canandaigua Lake—Rushville Quadrangles—Green's Landing—waterfall and adjacent shale banks along creek that flows across the Tamberlane Farm 1.6 km north of Cottage City.
14. Rushville Quadrangle—waterfall and adjacent shale banks along creek just east of intersection of U.S. Rte. 20 and Freshour Road.
15. Stanley—Geneva South Quadrangles—Benton Run—waterfalls and adjacent shale banks 0.8 km north of Reed Road and 360 m east of Pre-Emption Road.
16. Geneva South Quadrangle—Kashong Creek—high falls and adjacent shale banks 120 m south of Kashong Road and 1.4 km west of New York Rte. 14.
17. Dresden Quadrangle—waterfalls and adjacent shale banks along creek that crosses Old State Road 300 m from the road's southern intersection with New York Rte. 14.
18. Dresden Quadrangle—cutbanks along small creek flowing through Sampson State Park.
19. Ovid Quadrangle—Big Hollow Creek—shale banks and small quarry along creek 30-780 m west of Swick Road.
20. Ovid—Sheldrake Quadrangles—Mack Creek—high falls and adjacent shale banks along main creek and side tributary 0.6 km west of Rte. 89.
21. Ovid—Sheldrake Quadrangles—Bloomer Creek—high falls and adjacent shale banks along creek 0.5 km east of Rte. 89.
22. Ovid—Sheldrake Quadrangles—Barnum Creek—high falls and adjacent shale banks along creek 0.5 km west of Rte. 89.
23. Sheldrake Quadrangle—Grove Creek—cliff faces at Oak Tree Falls immediately south of Center Road 1.0 km east of Rte. 89.
24. Sheldrake Quadrangle—Powell Creek—high waterfall along creek 0.6 km east of Rte. 89.
25. Sheldrake Quadrangle—unnamed creek south of Powell Creek—waterfall and adjacent shale banks 0.6 km northeast of Rte. 89 and 1.4 km west of Sheldrake.
26. Sheldrake Quadrangle—Sheldrake Creek—steep falls and shale banks along creek adjacent to east-west county road connecting Rte. 89 and the town of Sheldrake.
27. Sheldrake Quadrangle—Beard Gully—high falls and shale banks along creek both east and west of Black Rock Road 1.9 km north of the town of Black Rock.
28. Sheldrake Quadrangle—steep falls along unnamed creek flowing into Cayuga Lake at Cats Elbow Point 1.2 km south of King Ferry Station.
29. Ludlowville Quadrangle—Salmon Creek—east-facing shale bank 120 m upstream from the bridge crossing the Salmon Creek Fishing Access Point 0.8 km south of Rte. 34B in the town of Myers.
30. Ludlowville Quadrangle—Portland Point—high cliff banks of Gulf Creek just east of Portland Point as well as exposures along the Lehigh Valley railroad cut 150 m south of Portland Point.
31. Scipio Center Quadrangle—second unnamed creek north of Ensenore Ravine flowing into Owasco Lake.
32. Owasco Quadrangle—east-facing roadcut along Rte. 38 at Cascade, New York.
33. Owasco Quadrangle—Champney's Quarry—abandoned small quarry northeast of the intersection of Rockefeller Road and Arnold Road.
34. Spafford Quadrangle—series of falls and adjacent shale banks along first unnamed creek north of Barber Gulf and adjacent to northernmost point along dirt road leading to Stag Horn Point.

Well-preserved favositid corals in the Oriskany Sandstone (Lower Devonian) of New York

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Abstract

Corals are rare in quartz sandstones of any age, and are particularly rare in the medium- to coarse-grained quartz sandstone facies of Pragian age in the Appalachians. The occurrence of well-preserved specimens of *Favosites* "*Emmonsia*" spp. in the Oriskany Sandstone in a local area of central New York provides the opportunity to re-analyze the Oriskany depositional environment and comment on the meaning of "*Emmonsia*." The preservation and details of occurrence of the corals suggest that they essentially grew where found. They were moved and, in many cases, overturned, but lived in the turbulent, nearshore depositional environment of the sandstone.

It is concluded herein that "*Emmonsia*" (emend.) is a morphologic stage in the development of many lineages of *Favosites* (emend.). However, the near-restriction of the morphology to the biogeographic Eastern Americas Realm indicates a more complex history. Either Eastern American and Old World *Favosites* were genetically different, or intrinsic or extrinsic factors caused the "*Emmonsia*" morphology to be preferentially expressed in the North American biogeographic area.

Favosites ("*Emmonsia*") *alternata* n. sp. with two morphologic variants (forms A and B) and *F. ("E.") congesta* n. sp. are described.

Introduction

Paleozoic corals are most commonly found in limestones and calcareous shales, but they can occur in almost any marine sedimentary rock. The more unlikely sources are coarse-grained quartz sandstone, such as the Oriskany Sandstone (Pragian, Lower Devonian) in central New York. The discovery of different species of well-preserved favositid corals at two levels in one exposure of the Oriskany Sandstone near the north end of Cayuga Lake (Figure 1) provides an opportunity to examine the tolerance of corals to extreme conditions. Additional interest derives from the fact that the Pragian was a low point in the history of Paleozoic corals; Pragian corals included relatively few genera and individuals, and the time marks the changeover from Lochkovian corals, which were similar to those of the Silurian, to the next great fauna of the Emsian to Frasnian Stages. The Lochkovian-Pragian boundary separates the Tippecanoe and Kaskaskia Sequences of Sloss (1963) and marks a major change in marine faunas.

The Oriskany coral fauna is of low diversity. Three (or four) species of *Favosites* ("*Emmonsia*") and rare *Favosites* s.s. (one known speci-

men) occur at two stratigraphic positions in the Oriskany Sandstone, and an additional species of "*Emmonsia*" occurs in the basal sandstone of the overlying Onondaga Limestone. Most of the specimens are from one locality, but three well-preserved "*Emmonsia*" and one rugose coral are known from nearby Oriskany localities (Figure 1). The specimens of "*Emmonsia*" spp. are described below, and it is concluded that the corals lived in the turbulent, nearshore environment of sandstone deposition.

This report agrees with earlier workers that "*Emmonsia*" is most likely a morphologic stage in the development of several lineages of *Favosites*, and that it should not be recognized as a genus-level taxon. However, the characteristic morphology is common in Emsian to Givetian coral faunas of the Eastern Americas Realm (EAR) and quite uncommon in the Old World Realm (OWR), where "*Squameo-favosites*" may hold an analogous position. This distribution pattern suggests either that EAR and OWR *Favosites* were genetically different, or that intrinsic or extrinsic factors caused the expression of different morphologies in the two realms.

Stratigraphic setting

The Oriskany Sandstone, in its type area in central upstate New York, is a light-colored, medium- to coarse-grained quartz sandstone, bounded above and below by unconformities (Figure 2). It is overlain by the Edgecliff Member of the Onondaga Limestone (Eifelian, Middle Devonian) and overlies the Manlius Limestone of the Helderberg Group (Lochkovian, Lower Devonian). In eastern New York, the interval between the Helderberg Group and the Onondaga Limestone is occupied by a wedge of mostly clastic rocks, the Tristates Group of Rickard (1975, p. 6, 8; 1981, p. 13). From oldest to youngest in east-central New York, the Tristates Group includes the Port Ewen Formation, the Oriskany Sandstone, the Esopus Shale, the Carlisle Center Shale, and the Schoharie Formation (Rickard, 1975, Pl. 3). Only the Oriskany Sandstone occurs west of Richfield Springs, but it is discontinuous, and in many sections the Onondaga Limestone rests directly on the Manlius Limestone or, west of Cayuga Lake, on formations of Silurian age.

In western New York and southwestern Ontario, the Bois Blanc Formation (Emsian) unconformably underlies the Edgecliff Member and overlies the discontinuous Oriskany Sandstone or the Silurian (Oliver, 1967). Between Buffalo and the Genesee Valley, the Bois

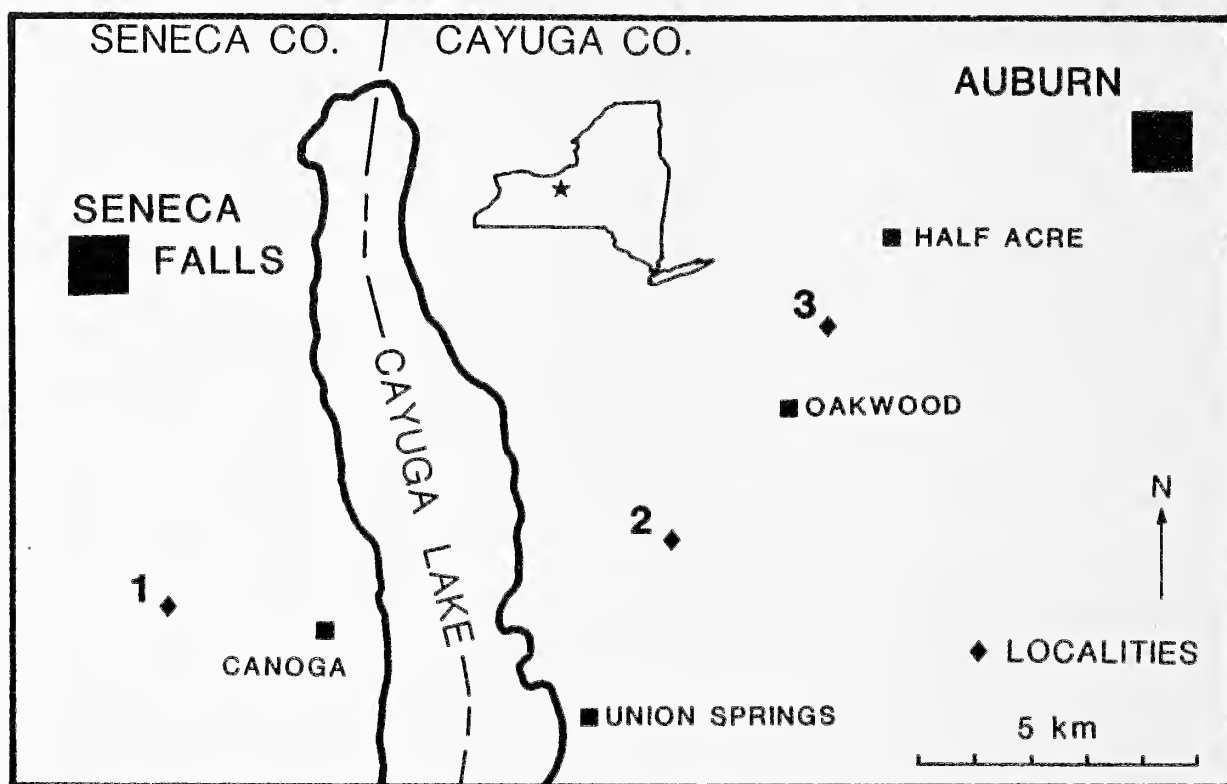


Figure 1. Index map of collecting area around the north end of Cayuga Lake in central New York. Cities and villages marked by squares, Oriskany Sandstone favositid localities by diamonds. 1, Seneca Stone Corp. quarry; 2, Yawger's Woods; 3, O'Hara's Woods. Star on inset map of New York shows general location of field area.

Blanc Formation is thin and discontinuous. Only a single outcrop is known east of the Genesee Valley. In both eastern and central New York, reworked sand derived from the Oriskany Sandstone locally forms basal sandstones in the Bois Blanc Formation (Springvale Sandstone) and/or the Edgecliff Member (Oliver, 1967). These basal sandstones are, in places, very similar to the Oriskany Sandstone and can be distinguished only with difficulty. The Springvale Sandstone (basal Bois Blanc) commonly contains Bois Blanc fossils that clearly separate it from the Oriskany Sandstone. In the central New York field area of this report, basal Edgecliff sandstones are recognized by their fauna or by the presence of phosphate nodules (see Hodgson, 1970, for description and discussion) at the contact with the Oriskany Sandstone. For purposes of this discussion, it is important to emphasize that three fossiliferous sandstones are recognizable in western and central New York: Oriskany, basal Bois Blanc, and basal Edgecliff. In the Cayuga Lake area, both the Oriskany and basal Edgecliff sandstones are present, and both contain specimens of "*Emmonsia*" spp., which are the subject of this paper.

Regionally, the coarse-grained quartz Oriskany Sandstone extends west from New York State to southwestern Ontario and south along the Appalachians to easternmost Kentucky, with an isolated patch in central Alabama (Oliver et al., 1968, p. 1004, fig. 6). Its greatest thickness (75-80 m) is in Maryland and adjacent parts of Pennsylvania and West Virginia. Throughout its outcrop belt, the Oriskany Sandstone is characterized by the "big-shell" brachiopod community of Boucot and Johnson (1967, p. 52), which is discussed below.

The Oriskany Sandstone is considered to be Pragian (=Siegenian) in age. Conodont evidence places it between the *delta* Zone (Lochkovian)

and *serotinus* Zone (Emsian) (see Kirchgasser et al., 1985, p. 236, for recent summary of data), but a Pragian age has long been accepted because of its well-known brachiopod fauna (see Rickard, 1975, p. 8, for review).

Local stratigraphy

Corals are rare in the Oriskany Sandstone, although molds of both favositids and rugosans (very rare) have been noted in association with the common brachiopods, less-common platyceratid gastropods, and a few other forms. The calcareous shell material is normally leached from outcrops, and most fossils are preserved as molds. Three localities near the north end of Cayuga Lake in Seneca and Cayuga Counties (Figure 1) are notable for the preservation of calcitic skeletal material and for yielding the only identifiable corals yet known from the formation. Geographic and stratigraphic data for the three localities are in Appendix 1; they occur along a 15 km stretch of the east-west outcrop belt on both sides of the lake. In this stretch, the maximum known thickness of the Oriskany Sandstone is 1.4 m, but it is absent at several localities. At one of the sites (Seneca Stone Corp. quarry; Figure 1, locality 1; Figure 3), "*Emmonsia*" specimens are common in both the lower and the upper parts of the Oriskany Sandstone and occur also in the basal sandstone of the Edgecliff Member. The quarry is active and the exposures are fresh; this adequately explains the preservation of calcareous fossils. Corals are not known to be common elsewhere in the Oriskany Sandstone, but two similarly preserved specimens of the same form of "*Emmonsia*" were collected at Yawger's Woods (Figure 1,

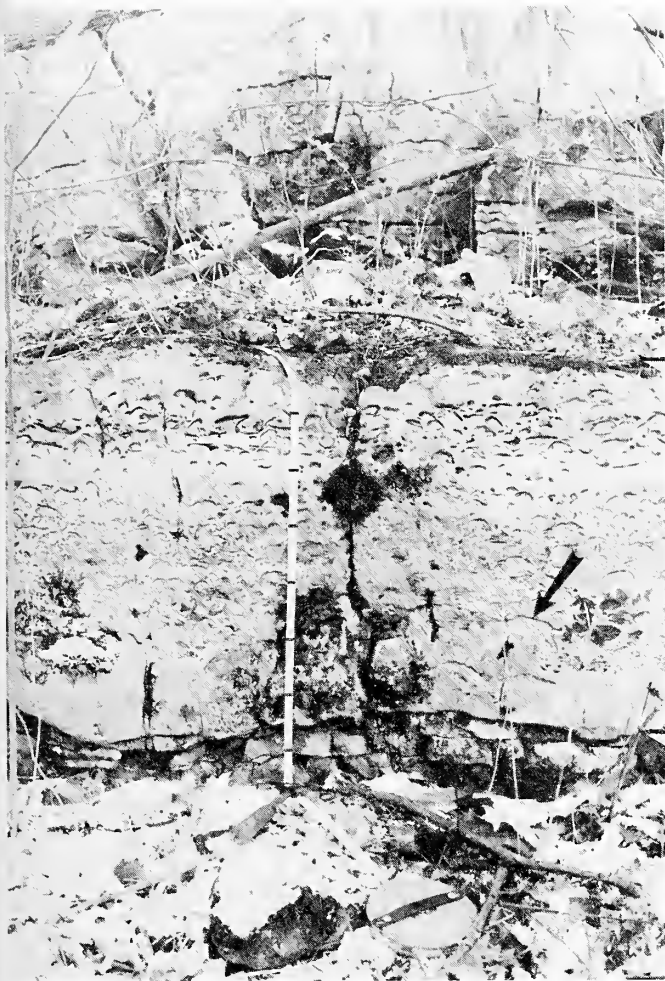


Figure 2. Outcrop at O'Hara's Woods. Typical stratigraphic sequence for the area, as discussed in text. Tick marks on tape are at 10 cm intervals. Massively weathering Oriskany Sandstone occupies the middle third of the photograph; upper and lower contacts are marked on right edge with Edgecliff Member above and Manlius Limestone below. The large *Favosites* ("Emmonsia") colony of Figure 5 is in the lower part of the photograph (black arrow). See Appendix for description of this section.

locality 2), and one specimen of another species was found at O'Hara's Woods (Figure 1, locality 3; Figure 2). The only identifiable rugose coral known from the Oriskany Sandstone ("*Heterophrentis*" sp.) was collected from a loose block within the same general area. Harris (1905, p. 4) noted, "A few coral fragments are found now and then" at Yawger's Woods, but the authors know of no other earlier reports of such occurrences.

In the Cayuga Lake area, the Oriskany Sandstone is less than 0.5 m thick. The local thickness of the basal Edgecliff sandstone varies from 0 to 3 m; it is 1.5 m at the Seneca Stone Corp. quarry. Except for the basal sandstone, the Edgecliff Member in the area is a light to dark grey, very coarsely crystalline limestone characterized by profuse rugose and tabulate corals (including numerous "*Emmonsia*") and some brachiopod and other shells in a matrix of crinoid debris; the thickness of this sandstone is approximately 3.0 m (Oliver, 1954, p. 626, 627). Where present, the basal Edgecliff sandstone commonly contains well-preserved Edgecliff corals and brachiopods. The pertinent sequence in

the Seneca Stone Corp. quarry (Figure 3) is as follows:

Onondaga Limestone

- 3.0 m (est.) Edgecliff Member, medium to dark grey coralline limestone with grey sandy limestone and calcareous sandstone forming the lower 0.5 m; fossils common.
- 0.1 m Reworked sand and phosphate nodules in dark grey limestone; *Favosites* ("*Emmonsia*") sp. 1 cf. *F. ("E.") emmonsii* is present; other corals, brachiopod valves, and crinoidal debris are locally common.

Oriskany Sandstone

- 0.6 m Very light grey, medium-grained quartz sandstone.
- 0.3 m Upper part of Oriskany is a big-shell (brachiopod) bed with *Favosites* ("*Emmonsia*") *congesta* n. sp. in upper part.
- 0.27 m Lower part of Oriskany is a sandstone with scattered *Favosites* ("*Emmonsia*") *alternata* n. sp., *Favosites* sp. (one specimen, USNM 449124), and brachiopod valves; the lower few cm contain fragments of the underlying limestone.

Manlius Limestone

Dark grey, fine-grained limestone; 1.5+ m exposed.



Figure 3. Exposure of Oriskany Sandstone in the Seneca Stone Corp. quarry. The "big-shell" bed and the basal contact with the Manlius Limestone are well-shown; contacts are marked on right edge by short black lines. See "Local stratigraphy" and Appendix for description. Tape in inches and feet.

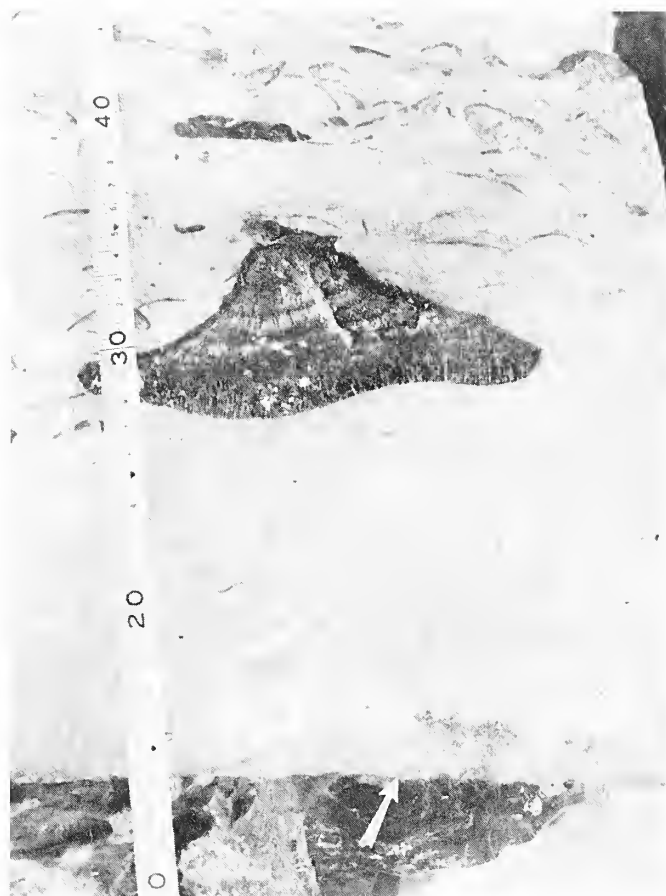


Figure 4. Upside-down *Favosites* ("Emmonsia") colony in the lower part of the Oriskany Sandstone in the Seneca Stone Corp. quarry. Arrow marks the contact between the Oriskany Sandstone and the underlying Manlius Limestone. Scale in centimeters.

The favositid corals from each of the three stratigraphic levels are distinct, although all but one are assigned herein to the form-subgenus "*Emmonsia*" in "Systematic paleontology."

Paleoecology

Earlier work

The Oriskany Sandstone was named by Vanuxem (1839, p. 273) in the Third Report of the New York Geological Survey. In his geology of the Third District, Vanuxem (1842) described the formation as consisting of medium-sized quartz sand and characterized by fossil shells of an unusually large size. The definitive description of the fossils is still Hall's (1859, p. 401-480). The fauna was termed the "Big-shell" Community by Boucot and Johnson (1967, p. 32) and renamed the *Hipparionyx* Community by Boucot (1975, p. 271). The common large brachiopods are *Acrospirifer*, *Costispirifer*, *Hipparionyx*, and *Reusselaeria*; other brachiopods, large *Platyceras*, bivalves, crinoidal debris, and *Tentaculites* are less common.

In analyzing the Oriskany depositional environment, Boucot (1982, p. 111) emphasized the coarse sediment "with largely disarticulated valves for those forms which disarticulate with ease," and "the absence of small specimens of those species represented by very large, robust specimens." Boucot suggested a "fairly turbulent, very well-oxygenated environment" and assigned the community to his Benthic Assemblage

(BA) 2, a medium-diversity, rough-water assemblage in a nearest-shore, subtidal setting (Boucot, 1982, pp. 91, 93, 111).

Barrett and Isaacson (1981) used a more quantitative approach to deal with the Oriskany environment in much greater detail. Their study area was the eastern outcrop belt in the Appalachians of northern West Virginia, Maryland, and southern Pennsylvania; this has been noted above as the area of greatest Oriskany thickness, but lithic and faunal characters are both similar to those of the thin New York unit. Barrett and Isaacson (1981) noted evidence of vertical community succession in the thicker sequence, but their environmental conclusions were similar to those of Boucot (1982): "the Oriskany Sandstone was deposited under shallow, nearshore, possibly littoral, marine conditions" (Barrett and Isaacson, 1981, p. 166).

This was not always the accepted interpretation. Clarke (1900, p. 78, 79) suggested that the large brachiopods in the Oriskany Sandstone "could not have had their habitat on such a deposit and in a sea whose depth favored such deposition." Instead of being inhabitants of this sandy facies, he interpreted the brachiopod assemblages as "agglomerations, swept out of their facies and away from the more calcareous, deeper-water deposits of the time" (Clarke, 1900, p. 79).

Corals in the lower part of the Oriskany Sandstone

In the Seneca Stone Corp. quarry, favositid colonies (mostly *Favosites* ("*Emmonsia*") *alternata* n. sp.) occur in the lower 27 cm of the Oriskany Sandstone with a horizontal spacing of 0.1 to 1 m along the vertical face of the ledge. Globular colonies that are more or less complete range in size from 2.5 by 3.8 cm (height by largest known diameter) to 12 by 30 cm. Some of the specimens are turned on their sides or are upside down (Figure 4), but some are in growth position. One small globular colony grew over the surface of a flat pebble of Manlius lithology that was incorporated into the base of the Oriskany Sandstone. The coral is conspecific with other lower Oriskany specimens, and apparently used the pebble for attachment while growing within the Oriskany environment; the pebble is parallel to the bedding, and the coral is in growth position.

At least one colony has a tabular-lenticular shape. Its preserved dimensions are 4.0 cm (height, tapering laterally to less than 2.0 cm) by 13 cm (diameter). The specimen may represent the marginal part of a much larger colony, but whether it was originally larger or not its shape and thin margins indicate that it is unlikely to have been overturned or transported far.

The largest known colony in the lower Oriskany Sandstone is a *Favosites* ("*Emmonsia*") sp. 2 cf. F. ("*E.*") *emmonsii* Hall, collected at O'Hara's Woods (Figures 2, 5). The colony is approximately 20 cm high and 60 cm long in the outcrop and is in growth position.

Large, disarticulated brachiopod valves are scattered through the same beds. These have not been studied, but the valves seem to be reasonably complete, with little evidence of the damage expected from extensive transport.

All of these observations are compatible with Boucot's (1982, p. 111) "fairly turbulent, very well-oxygenated environment." Many of the corals were overturned or moved, and some damage was sustained. However, the evidence indicates that they did not move very far, that some are preserved in growth orientation and probably location, and that the corals and brachiopods both lived and grew in the depositional environment of the sandstone.

Corals in the upper part of the Oriskany Sandstone

The upper 12 cm of the Oriskany Sandstone at the Seneca Stone Corp. quarry is almost a coquina of brachiopod valves (Figure 3, the

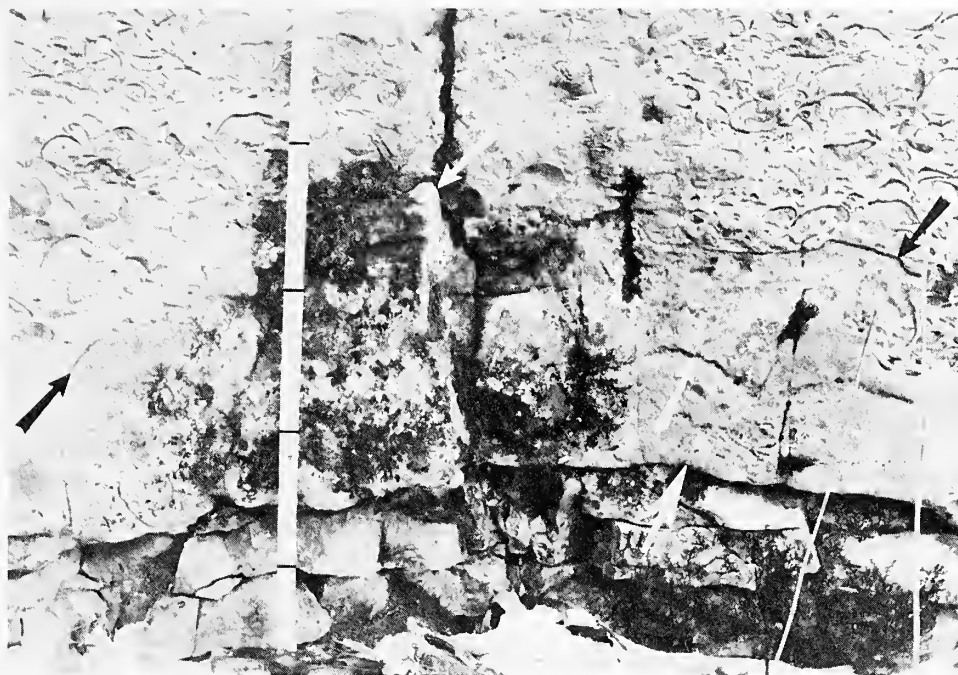


Figure 5. Large colony of *Favosites* ("Emmonsia") sp. 2 cf. *F. ("E.") emmonsii* Hall in lower Oriskany Sandstone at O'Hara's Woods. Colony is 60 cm long and 20 cm high in the outcrop. Sampled part of colony (marked by uppermost white arrow) is USNM 449108; see Figure 2 and Plate 3, figures A-D. Large white arrow points to the base of the Oriskany Sandstone. Tape shows 10 cm units.

"big-shell" bed), although shell concentrations change over a short distance laterally. Within the shell bed, especially where the shells are more widely scattered, are numerous specimens of *Favosites* ("Emmonsia") *congesta* n. sp. The coralia are apparently all incomplete, but fragments from 1.0 cm up to 4.0 cm high and 8.0 cm in diameter are known. All studied specimens belong to *F. ("E.") congesta* n. sp. and are quite different from the forms in the lower Oriskany Sandstone or basal Edgecliff Member.

The shell concentration and the fragmentary, apparently disoriented corals indicate a greater turbulence during deposition of the upper beds than is suggested for the lower beds. The shell bed indicates some winnowing, and none of the corals or brachiopods grew where they are now found. The shells are reasonably whole, and it seems more likely that they were concentrated by wave and current action and were not transported significant distances from where they grew.

Corals in the basal part of the Edgecliff Member

One *favosites* ("Emmonsia") colony (*Favosites* ("E.") sp. 1 cf. *F. ("E.") emmonsii* Hall) was collected loose in the Seneca Stone Corp. quarry, but clearly came from the basal sandstone of the Edgecliff Member, because the matrix matches this unit very closely and the coral is similar to an Edgecliff species. The specimen is a part of a small(?) tubular-lenticular colony; the maximum preserved height of 16 mm tapers to 2.0 mm in a lateral distance of 8.0 cm, and the maximum diameter is 12 cm. The complete colony may have been much larger, but the preservation of such a thin edge strongly suggests that the colony is preserved in growth position. Other corals, brachiopod valves, and pelmatozoan stem plates are associated with the "Emmonsia" specimen and contribute to an understanding of the environment.

The basal Edgecliff sandstone apparently originated as the transgressive Onondaga Sea overlapped across the surface of the eroded Oriskany Sandstone. Phosphate nodules suggest that there may have been a long

period of minimal erosion or nondeposition. The advancing Onondaga Sea reworked some of the sand and nodules, and a few Onondaga fossils have been preserved in this initial deposit. The early Edgecliff environment may not have been very different from that of the Oriskany Sandstone, and was probably turbulent and well-oxygenated.

Summary

At three different stratigraphic levels in the Seneca Stone Corp. quarry, well-preserved specimens of *Favosites* ("Emmonsia") spp. occur in sandstones. This is a very unusual association, but the evidence suggests in each case that the corals lived essentially where found and that they grew very well in what must have been submarginal conditions for most corals.

Biogeography

Specimens and species of "Emmonsia" are most common in eastern North America; the Oriskany Sandstone species are the first to be described of Pragian age, but the "subgenus" occurs in rocks of Pridolian and Lochkovian ages and is common or abundant in coralliferous facies of Emsian to Givetian age. Elsewhere, "Emmonsia" is known from Nevada (Lochkovian?, Pragian, Emsian), Venezuela (late Emsian or early Eifelian), and the Eifelian of Spain and the Urals (see "Systematic paleontology" for references and discussion).

The Early and Middle Devonian world was markedly provincial, and the corals were among the most provincial of marine animals (Oliver, 1977; Oliver and Pedder, 1979, 1989). Almost all discussions of Devonian coral biogeography have been based on rugose corals, but endemic tabulates have been noted (Oliver, 1975), and there is no reason to think that tabulate distribution patterns are very different. For the Early and Middle Devonian, three marine biogeographic realms are rec-

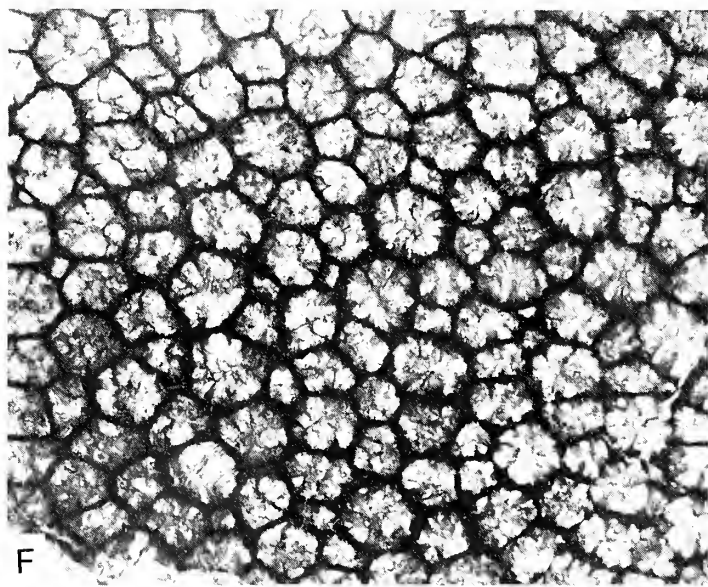
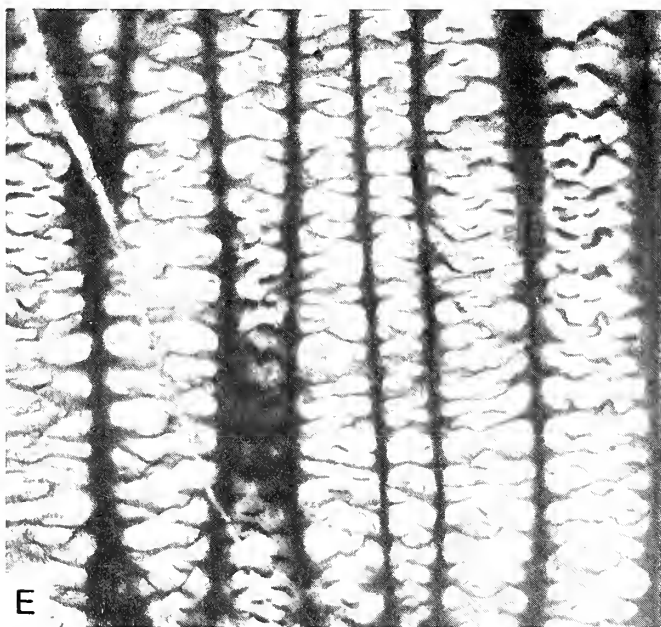
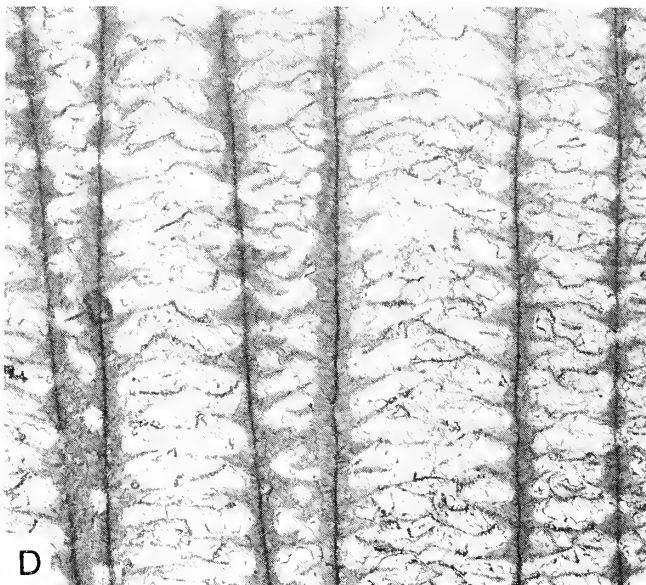
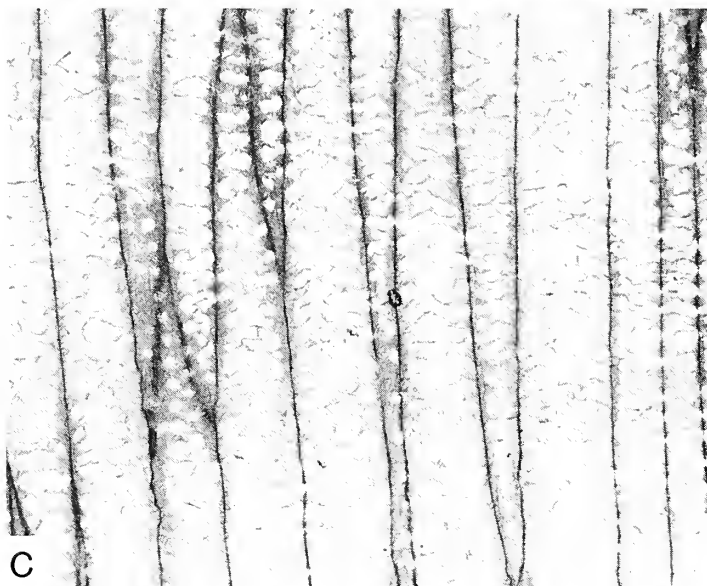
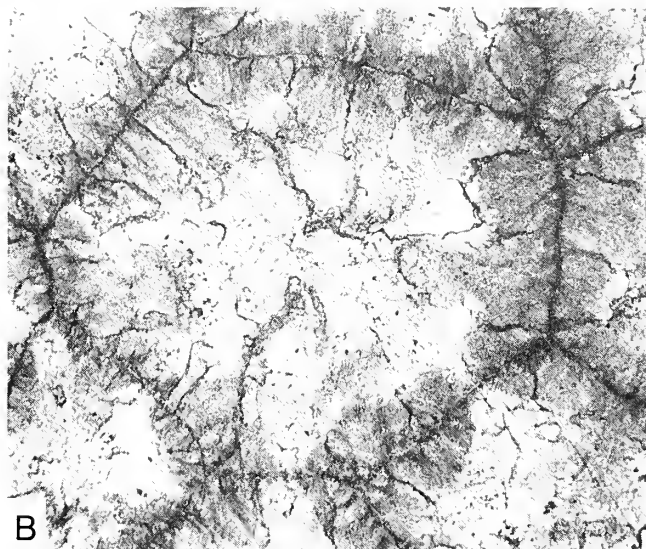
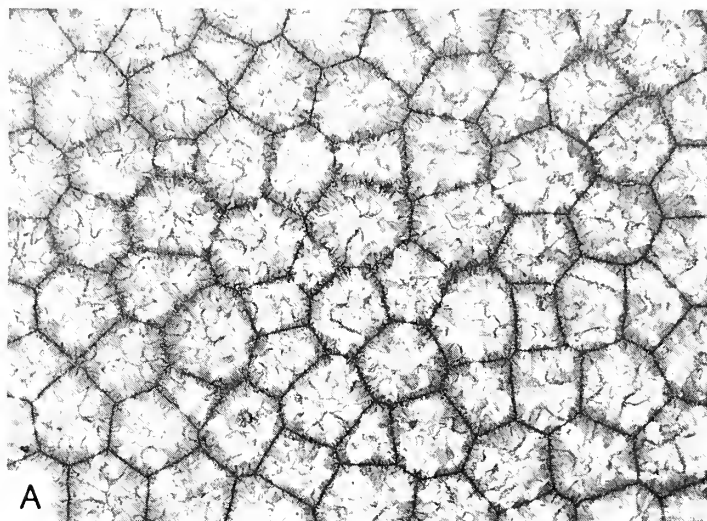


Plate 1. *Favosites* ("Emmonsia") *emmonsii* Hall, 1877, and Rominger, 1876. A-D, F. ("E") *emmonsii* Hall, lectotype, NYSM 6216, Williamsville, New York, probably reef facies Edgechiff Member, transverse and longitudinal thin sections, x5, x25, x5, x10, respectively. E-F, F. ("E") *emmonsii* Rominger, lectotype, UMMP 8449, Jeffersonville Limestone, Charleston Landing, Indiana; longitudinal and transverse thin sections, x10, x5, respectively.

ognized. The Eastern Americas Realm (EAR) included most of eastern North America east of the Transcontinental Arch and south of the Canadian Shield. During the Pragian and early Emsian, it extended west to include the Great Basin Province, and during the late Emsian or early Eifelian to Givetian(?), it included the Venezuelan-Colombian Province (Oliver, 1989, p. 3-4). All other tropical to temperate marine areas with good coral faunas belonged to the Old World Realm (OWR). The third realm (Malvinokaffric) was very poor in corals.

The distribution of "*Emmonsia*" is similar to that of some rugosan genera that seem to have originated as EAR endemics. It could have originated in the EAR, presumably from one or more species of *Favosites*. "*Emmonsia*" thrived there to the end of the Givetian when it, along with other endemics, became extinct. It may have migrated to the Great Basin and to Venezuela when those areas were parts of the EAR. In the Eifelian, it migrated out of the EAR into Spain, presumably by way of northwestern Africa, and on across the European plates to the Urals. Such a pattern is very similar to those of some rugose corals discussed by Oliver and Pedder (1989).

This possible history may or may not be compatible with our interpretation of "*Emmonsia*" as a form-subgenus. In the "Systematic paleontology," this report agrees with earlier workers who have found "*Emmonsia*" to be a morphologic stage in the development of many lineages of *Favosites* and unacceptable as a generic-level taxon. It is useful primarily because of its morphologic implications. However, the geographic distribution suggests additional interpretations. Possibly an EAR population of *Favosites* developed the "*Emmonsia*" genetic tendency that was expressed when extrinsic or intrinsic factors were "right." The rare Old World "*Emmonsia*" may reflect either the rareness of the hereditary component in Old World *Favosites* or a pattern of migration from the EAR as suggested above. It is notable that most Old World Realm squamulate *Favosites* are "*Squameofavosites*" (see discussion in "Systematic paleontology"), which may be the Old World analog of "*Emmonsia*."

Systematic paleontology

Genus FAVOSITES Lamarck, 1816, emend.

Type species.—*Favosites gothlandicus* Lamarck, 1816.

Emended diagnosis.—Cerioid tabulate corals that develop massive or branching colonies; prismatic corallites closely appressed with thin to moderately thick walls; communication through walls by mural pores that tend to have a species-diagnostic diameter and are arranged in one or more longitudinal rows; septa may be lacking or represented by longitudinal rows of bumps, spines and/or squamulae; tabulae complete or incomplete, subhorizontal. (Partly based on Oekentorp, 1975, p. 13.)

Discussion.—Some authors (e.g., Hill, 1981) have recognized subgenera or genera based on the absence, presence, or prevalence of squamulae. This report agrees with those who have interpreted "*Emmonsia*," at least, to be a morphologic stage in the development of many *Favosites* lineages and unacceptable as a generic-level taxon. However, "*Emmonsia*," with numerous to abundant squamulae and virtually no spines, is common in the EAR and uncommon elsewhere, whereas "*Squameofavosites*," with both spines and squamulae, is common in the OWR and not known to occur in the EAR Devonian. Within the EAR, "*Emmonsia*" ranges in age from Pridolian to Givetian and is particularly abundant in rocks of Emsian to Givetian age. "*Squameofavosites*" occurs in the Pridolian but apparently becomes extinct in the EAR before the Devonian. In contrast, "*Emmonsia*" is absent, rare, or

uncommon in different parts of the OWR where "*Squameofavosites*" ranges from the Upper Silurian to lower Middle Devonian (Hill, 1981, p. F557). It is convenient to use the term "*Emmonsia*" in a descriptive sense; many earlier workers have made similar use of both "*Emmonsia*" and "*Squameofavosites*."

Form-subgenus "EMMONSIA"

Milne-Edwards and Haime, 1851, emend.

1851 *Emmonsia* Milne-Edwards and Haime, p. 152, 246-247.

in part, 1876 *Favosites*, Rominger, p. 19-21 ("...a character so changeable...cannot be used as a generic distinction..."). (?) Suggested septal origin of squamulae (p. 28).

in part, 1877 *Favosites*, Hall, expl. Pls. 1-13.

in part, 1879 *Favosites*, Nicholson, p. 37-45 ("...the separation of *Emmonsia* as a distinct genus cannot be carried out in practice," p. 41).

1889 *Emmonsia*, Miller, p. 187, ("generally regarded as a synonym" of *Favosites*).

1925 *Emmonsia*, Smith and Gullick, p. 116-117, 119 ("polyphyletic").

1936 *Emmonsia*, Fenton and Fenton, p. 22-23 ("polyphyletic").

1938 *Emmonsia*, Stewart, p. 67 (notes on p. 38 that "intermediate species" are "difficult to determine").

1940 *Emmonsia*, Lang, Smith, and Thomas, p. 56.

1947 *Emmonsia*, Swann, p. 264-262 ("polyphyletic genus").

Convincing discussion of septal origin of squamulae (p. 250-252).

1949 *Emmonsia*, Stumm, card 187 (cards 188-218, mostly by Stumm, are a comprehensive analysis of the "genus" in North America).

1952 *Emmonsia*, Lecompte, p. 513 (in new Subfamily Emmonsiniinae).

1953 *Favosites* {*Emmonsia*}, Ross, p. 49 ("genomorph"="morphologic stage" of *Favosites*).

not? 1954 *Emmonsia*, Fontaine, p. 57.

in part?, 1955 *Emmonsia*, Flügel, p. 272-275.

1956 *Emmonsia*, Hill and Stumm, p. F464.

1959 *Emmonsia*, Yanet, p. 107 (in Subfamily Emmonsiniinae).

in part, 1960 *Favosites*, Philip, p. 190-193 (good discussion of squamulae).

1962 *Emmonsia*, Sokolov, p. 223 (in Subfamily Emmonsiniinae).

?1963 *Emmonsia*, Dubatolov, p. 54-55 (in Subfamily Emmonsiniinae).

1964 *Emmonsia*, Stumm and Tyler, p. 28.

1964 *Emmonsia*, Stumm, p. 65-68.

in part, 1973 *Emmonsia*, Scrutton, p. 272.

1974 *Favosites* (*Emmonsia*), Schouppé and Oekentorp, p. 168-172.

1975 *Favosites* (*Emmonsia*), Oekentorp, p. 34-56 (this, and the preceding, are among the most useful recent discussions of the *Favosites* complex).

1981 *Emmonsia*, Hill, p. F551-353; (in Subfamily Emmonsiniinae Lecompte).

1985 *Emmonsia*, Birenheide, p. 65-66 (recognized genus, but not subfamily).

Discussion.—The above list is not a synonymy in the ordinary sense. Rather, it is an annotated list of works important in understanding the history and usage of "*Emmonsia*" as a taxon and/or morphologic stage in the development of several *Favosites* lineages. Few authors prior to 1949 seem to have accepted it as a genus or subgenus in the sense of an implied monophyletic origin. Both Rominger (1876) and Hall (1877) were aware of the name, but neither found it useful. Stewart (1938) used the genus with reservations, but Lecompte (1952) not only used it but based a new subfamily on it. Hill and Stumm (1956) recognized the genus, and Sokolov (1962) accepted the subfamily, as did Hill

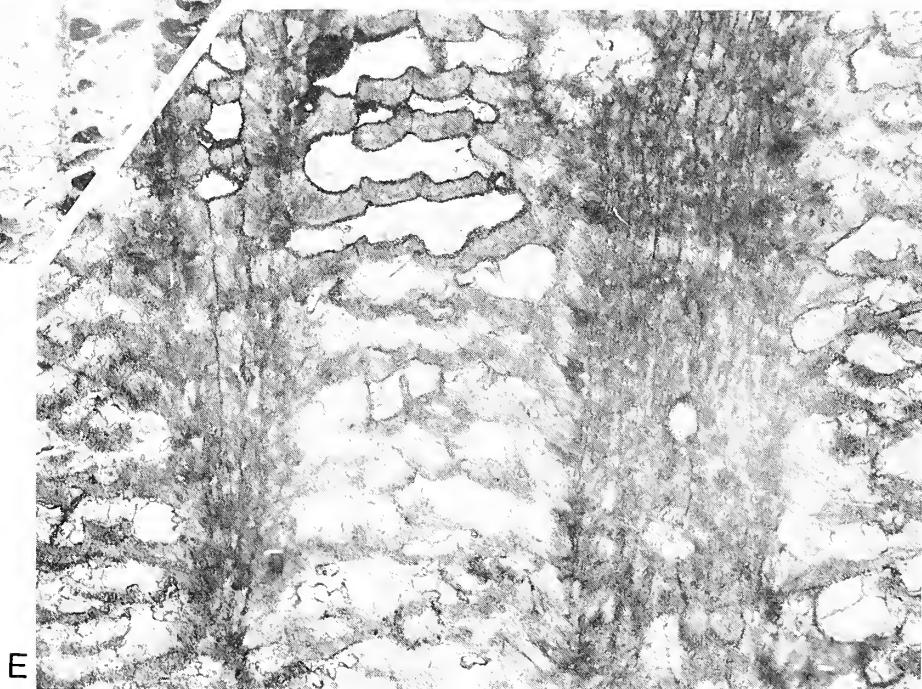
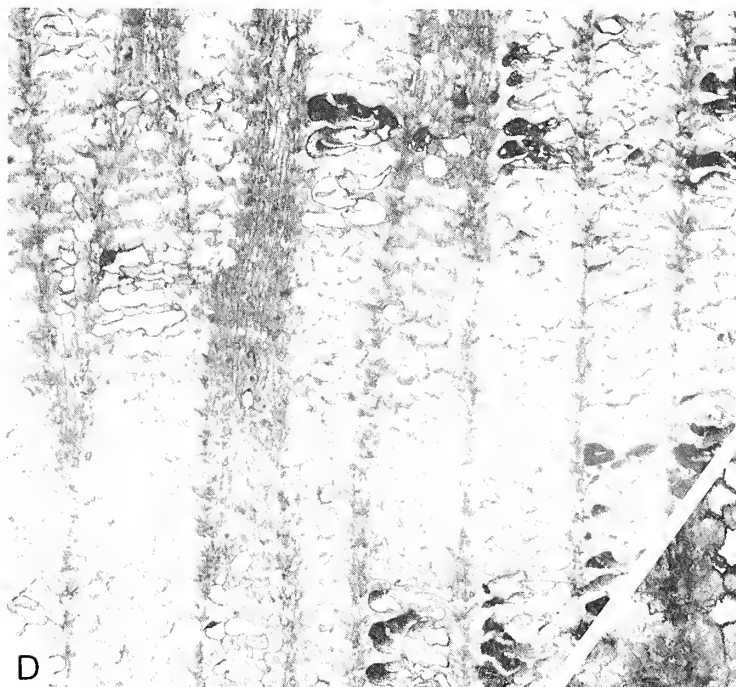
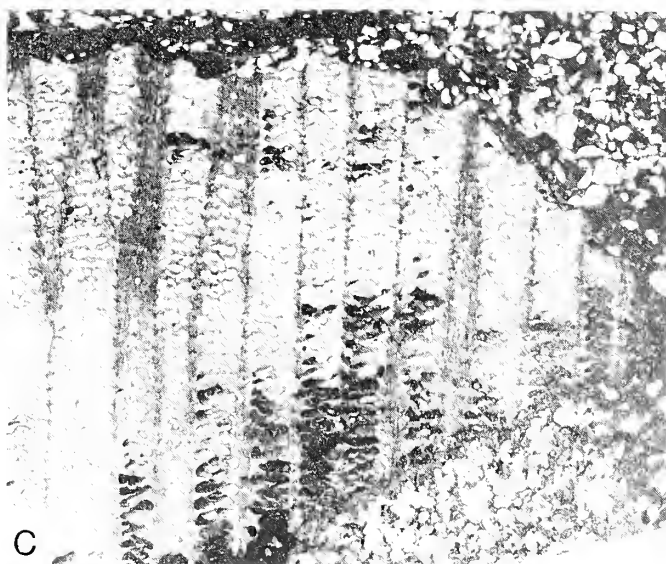
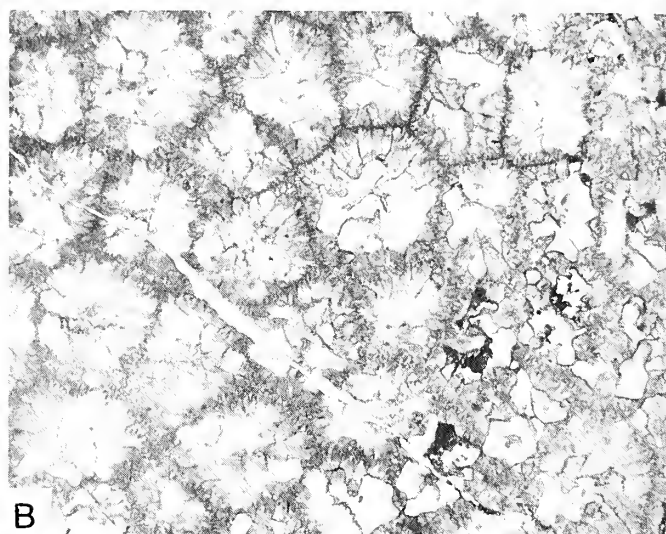
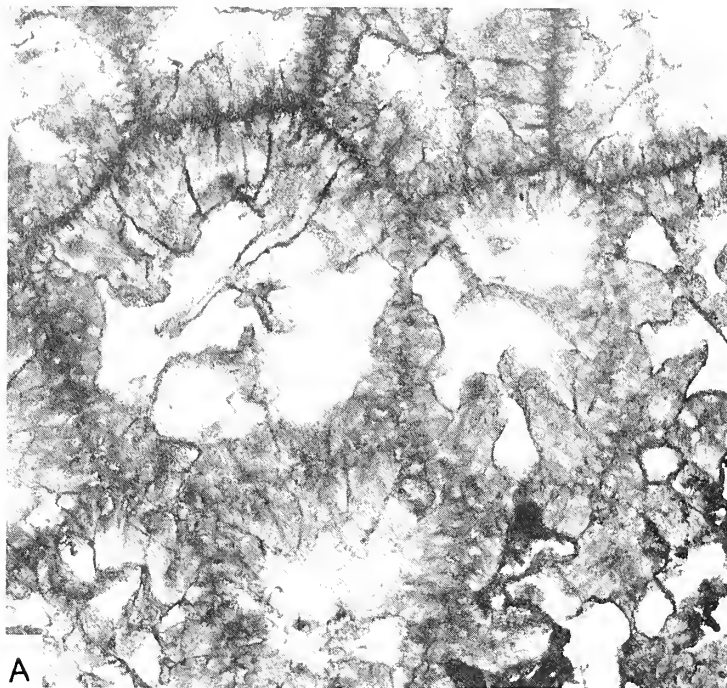
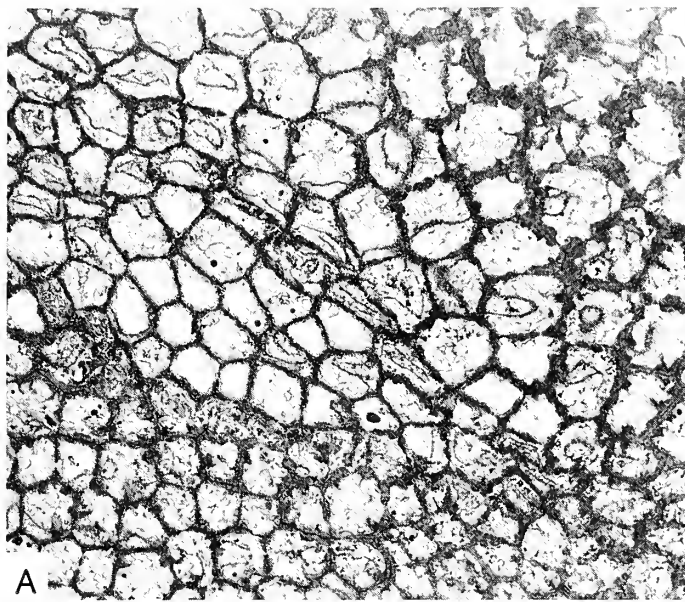
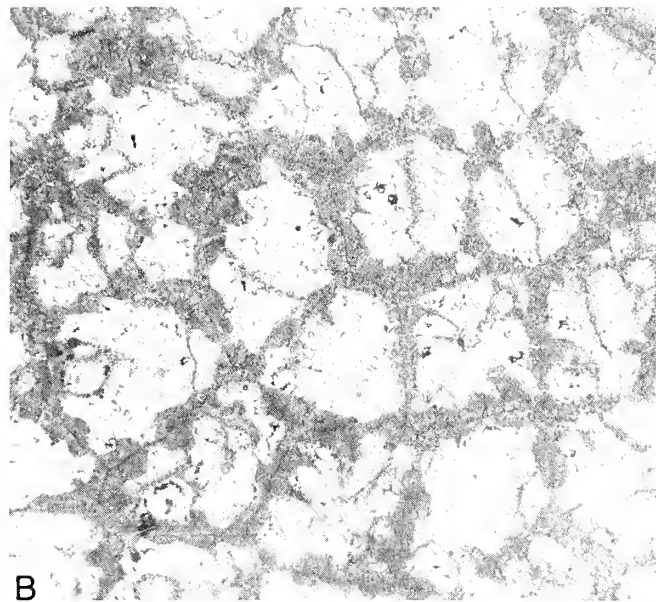


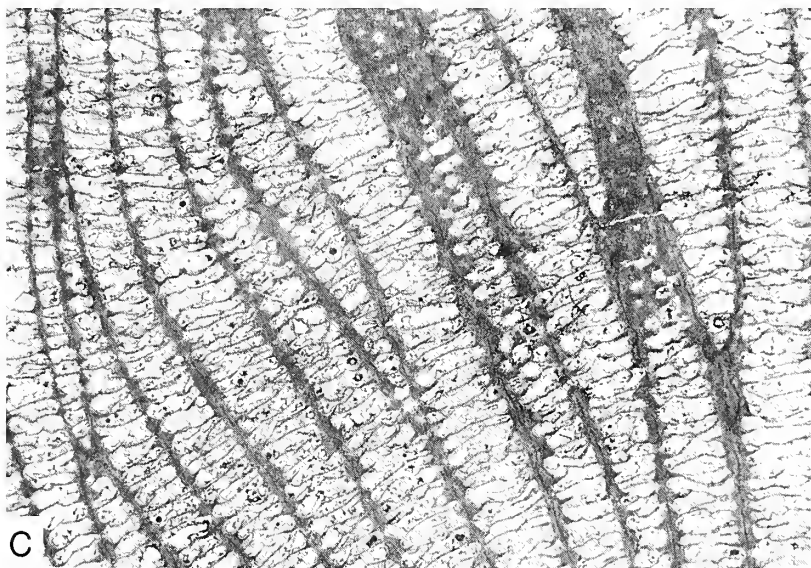
Plate 2. *Favosites* ("Emmonsia") sp. 1 cf. *F. ("E.") emmonsii* Hall. USNM 449104, basal sandstone of the Edgecliff Member, Seneca Stone Corp. quarry, USGS collection 10436-SD. A-E, transverse and longitudinal thin sections, x25, x10, x5, x10, x25, respectively.



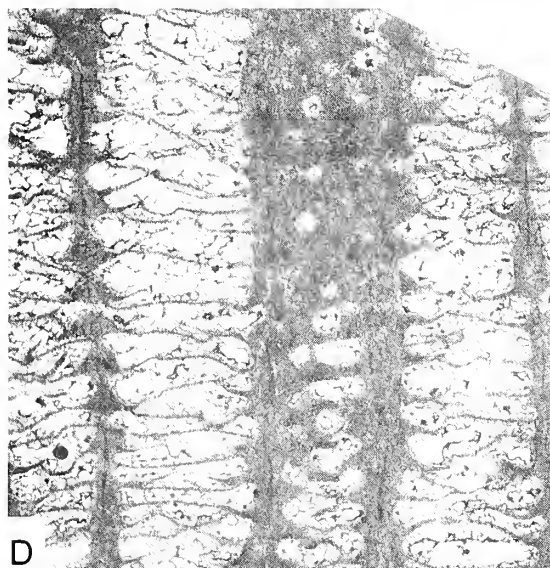
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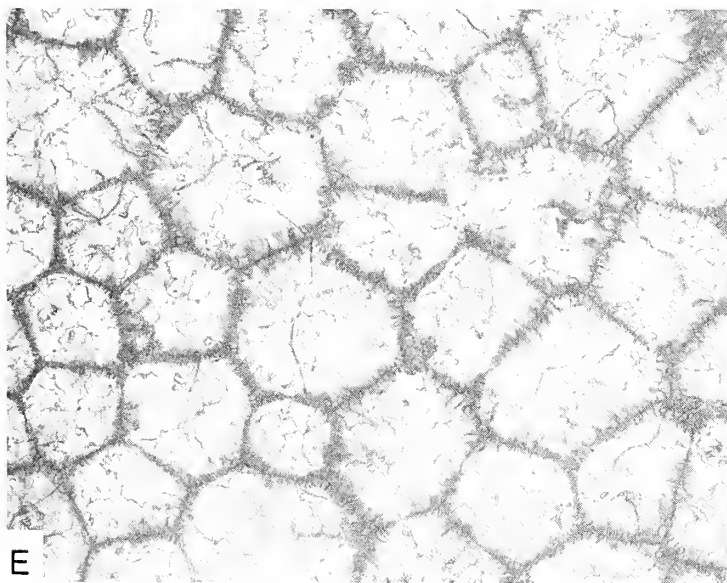
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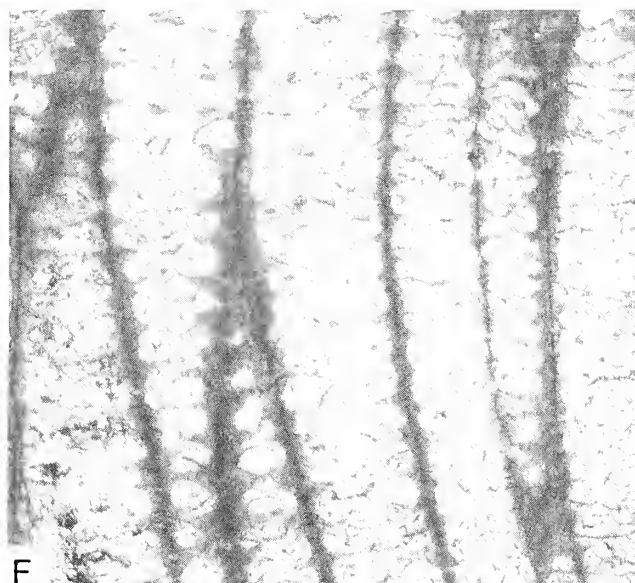
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E



F

Plate 3. *Favosites* ("Emmonsia") spp. cf. *F. ("E.") emmonsii* Hall. A-D, F. ("E.") sp. 2 cf. *F. ("E.") emmonsii*, USNM 449108, lower Oriskany Sandstone, O'Hara's Woods, transverse and longitudinal thin sections, x5, x10, x5, x10, respectively; see also Figures 2, 5. E-F, F. ("E.") sp. 1 cf. *F. ("E.") emmonsii*, USNM 449107, non-reef Edgecliff Member, Cobleskill, N.Y.; transverse and longitudinal thin sections, x10.

in the 1981 revision of the *Treatise on Invertebrate Paleontology*, Part F. The principal usage has been in compendia of genera where the proper emphasis has been on the recognition of morphologic entities. However, there seems to be no general agreement on the meaning or usefulness of the name.

Type species.—*Emmonsia hemispherica* (Yandell and Shumard) of Milne-Edwards and Haime, 1851, not *Favosites hemispherica* of earlier workers as Milne-Edwards and Haime supposed. Lang et al. (1940, p. 56) discussed the complex route by which the type species became *Favosites emmonsii* Hall (1877, see explanation of Pls. 9, 11, 12), as restricted by Fenton and Fenton (1936, p. 35-36), who selected the original of Hall, 1877, Pl. 12, fig. 5, as lectotype (NYSM 6216; see Plate 1, figures A-D). Most authors have considered Hall's (1877) *F. emmonsii* to be conspecific with *Favosites emmonsii* Rominger (1876, p. 27-28), as restricted by Stumm (1964, p. 66). Stumm (1964) selected Rominger's (1876, Pl. 7, fig. 1) original as lectotype (UMMP 8449; see Plate 1, figures E-F). This report tentatively agrees with this selection. However, it is important to note that there are morphologic differences between the two lectotypes, that they are from different biogeographic provinces, and that they may be of different ages.

The possibility that these lectotypes represent different species cannot be ruled out. This opinion is based on examination of the lectotypes and eight additional specimens that may or may not be conspecific; the whole complex of "*Emmonsia*" spp. needs revision, but such a project is beyond the scope of this report. The intention herein is not to redescribe the species but to emphasize that anyone who uses the genus must base the concept on Hall's specimen. This report considers the two lectotypes to belong to the same genus, either *Favosites* or "*Emmonsia*," and the distinction has no general significance except to those who accept "*Emmonsia*" as a valid generic-level taxon or are doing species-level work in eastern North America.

Part of the confusion has resulted from Hall's initial error of citing his specimen as being from the Falls of the Ohio near Louisville, Kentucky (Hall, 1877, explanation of Pl. 12, fig. 5). Labels on the specimen and the Locality Register of the New York State Museum (NYSM) are almost certainly correct in giving the provenance as "Onondaga Limestone, Williamsville, Erie Co., N.Y." Rominger's specimen is from the lower part of the Jeffersonville Limestone at "Charleston Landing, Indiana" (Stumm, 1964, p. 154), near Louisville. The New York and Indiana-Kentucky localities have many species in common, so this is not an argument for the lectotypes being from different species, but the assumption that they were both from the Falls area of the Ohio River has no doubt made later workers less critical.

Internal evidence in Hall (1877) indicates his recognition of the priority of Rominger's work (e.g., Hall, 1877, explanation of Pl. 8; see also Stumm, 1948; and Oliver, 1987, p. 100, 101, for discussions). Hall almost certainly intended to credit Rominger "ined." (i.e., "in press") with the species' name, as he did for many other names in the same report. This conclusion is further supported by the fact that the Hall and Rominger synonymies are similar and the names identical. However, through error or otherwise, Hall termed the form a "n. sp.", with no mention of Rominger. Thus *Favosites emmonsii* Hall is a valid name, although a junior homonym of *F. emmonsii* Rominger. It may be a synonym also, but the Hall specimen is the ultimate basis for the generic-level name when used.

Provenance of lectotype.—"Onondaga Limestone, Williamsville, Erie Co., N.Y." (Clarke, 1908, p. 130). The specimen is almost certainly from the Edgecliff Member of the Onondaga Limestone at the old Fogelsanger Quarry on the west side of Williamsville (late Emsian or

early Eifelian age). Although the locality was destroyed by highway construction some years ago, collections are to be found in many museums, and a reviser should have no difficulty in finding topotype material.

Emended diagnosis.—*Favosites* in which septa are represented by squamulae; septal spines absent or very rare.

Discussion.—Squamulae are plate- or tongue-like projections from the corallite wall in various favositoid corals; available descriptions and illustrations are in Hill (1981, p. F445). Many early workers considered squamulae to be incomplete or degenerate tabulae, but Rominger (1876, p. 28) described them as "imperfect septa", and Swann (1947, p. 250-252) and Philip (1960, p. 190-192) demonstrated their septal origin.

Squamulate *Favosites* include "*Squamofavosites*," with septal spines and squamulae, in addition to "*Emmonsia*." However, this report is concerned only with "*Emmonsia*," and simply notes that "*Squamofavosites*" is a characteristic Old World form as yet unknown in the EAR Devonian.

EAR distribution.—Eastern Americas Realm: Pridolian to Pragian (in Appohimchi Province), Emsian to Givetian (common to abundant and widespread in both the Appohimchi and Michigan Basin Provinces); late Emsian or early Eifelian in Venezuela (Scrutton, 1973, p. 273-275, Pl. 10, figs. 1-6); Pragian-Emsian in Nevada (Great Basin Province), discussed below.

Pre-Emsian "*Emmonsia*" have not been reported previously, but available prepared collections were analyzed with the following results:

Pridolian: "*Emmonsia*" was identified from the Keyser Formation of the central Appalachians (Virginia), but it seems to be uncommon or rare. "*Squamofavosites*" appears to be much more common. It was identified from the Keyser Formation in the same general area (Virginia, West Virginia, Maryland, and south-central Pennsylvania), the Decker Formation (New Jersey), and the Glasco Member of the Rondout Formation and the Cobleskill Limestone (New York). No "*Squamofavosites*" have been recognized in Devonian rocks of the EAR.

Lochkovian: One specimen of a massive "*Emmonsia*" is known from the bioherm facies of the Coeymans Limestone in central New York. Several specimens of one species of a ramose "*Emmonsia*" are known from Coeymans bioherms at two or more localities. The distal corallite walls are thickened in these specimens, and the species is congeneric with *Favosites digitatus* Rominger if that species has squamulae, as stated by Rominger (1876, p. 39). Rukhin (1937, p. 11) made Rominger's species the type of *Dendrofavosites* Rukhin and assumed the presence of squamulae (see Hill, 1981, p. F553, for further comments). Conceptually, at least, "*Dendrofavosites*" would be to "*Emmonsia*" as *Thamnopora* is to *Favosites*.

Stumm (1949, card 193-194) referred the ramose *Favosites conradi* Girty, 1895 (Lochkovian, New York), to *Emmonsia*?, but Girty's description and illustrations are more of a branching *Favosites*, with twelve rows of septal spines, than an "*Emmonsia*." Girty's specimens are apparently lost, and the species is unrecognizable.

Pragian: The Oriskany Sandstone species described herein are the only ones now known from Pragian rocks in eastern North America. See below for discussion of Great Basin Province.

Emsian and later: Many species from the Jeffersonville (Coral Zone) and "Onondaga" Limestones that were described during the 19th and early 20th centuries are of Emsian age (see Oliver, 1976, p. 5-12, for discussion), but reevaluation of these species has barely begun, and most ranges are unknown. However, "*Emmonsia*" is present or common in the Bois Blanc Formation (Emsian, western New York) and common to abundant in the Edgecliff Member of the Onondaga Limestone (late Emsian or early Eifelian, New York). The lectotype of

Favosites ("E.") *emmonsii* Hall is from the Edgecliff Member. Later Eifelian and Givetian occurrences are well-documented by Swann (1947) and Ross (1953).

OWR distribution.—Old World Realm forms are known from the Eifelian of Spain (Oekentorp, 1975, p. 56-62, Pls. 10-12) and the Urals (Yanet, 1959, p. 107-109, Pl. 49, figs. 1a-2, unnumbered Figs.; and possibly in Dubatolov, 1963, p. 54-56, Pl. 21, figs. 3a-d, unnumbered Figs.). Reported occurrences in the Emsian(?) of Vietnam (Fontaine, 1954), the lower Middle Devonian of Turkey (Flügel, 1955), and the Devonian of China (Tchi, 1987) are not convincing. "*Emmonsia*" has been reported from North Africa (LeMaitre and Poueyto, 1955; Sougy, 1964) without supporting descriptions or illustrations. However, Middle(?) Devonian collections from the Western Sahara in the U.S. National Museum include both massive and ramose "*Emmonsia*."

No "*Emmonsia*" specimens have been described from western North America, but an unpublished dissertation by Flory (1975) cited and illustrated one species of "*Emmonsia*" and several of "*Squamofavosites*" (some of which may be "*Emmonsia*") from the Great Basin. In addition, a few specimens of "*Emmonsia*" have been identified in USGS collections from the same area. The results of an analysis of these two sources are as follows: late Lochkovian, questionable; Pragian, confirmed by specimens; Emsian, probable; no Middle Devonian forms are known. During the Pragian and early Emsian, the Great Basin Province was a part of the EAR, but if Lochkovian "*Emmonsia*" are confirmed this would suggest a common origin from geographically widespread Pridolian forms rather than migration from eastern North America.

Oriskany "Emmonsia".—The species described in the following sections are the oldest yet described, although still older species are known (see EAR distribution). *Favosites* ("*Emmonsia*") *alternata* n. sp. is from the lower half of the sandstones; it is characterized by thin squamulae and tubular that are distinctly zoned. Two forms are described that differ in corallite size and in the nature of the zonation.

Favosites ("*Emmonsia*") *congesta* n. sp. is from the upper "big-shell" bed of the sandstone; it differs from *F.* ("E.") *alternata* in having grossly thickened squamulae. The two Oriskany species are distinct in the available samples, and the contrast between colonies from the lower and upper beds is striking. They are unlike other described "*Emmonsia*."

Two other specimens from sandstones are separately described as *Favosites* ("*Emmonsia*") sp. 1 and 2 cf. *F.* ("E.") *emmonsia*. One is from a medium to medium dark grey calcareous sandstone that contrasts with the very light grey sandstone of the Oriskany Sandstone proper. The source is the basal beds of reworked sand in the Edgecliff Member of the Onondaga Limestone. Such beds are known in the Seneca Stone Corp. quarry and in many other sections in the area. The second is from the lower Oriskany Sandstone at O'Hara's Woods, and is quite different from other known Oriskany species.

Corallite diameter varies in the described specimens from very small in new offsets (commonly with three or four sides) to a maximum in mature corallites (with five to seven sides). The variation is continuous, and it is not feasible to separate immature, expanding corallites from mature, prismatic ones. Any measure of diameter is of questionable value, but the larger or largest diameters are considered herein to be the most useful. In the descriptions, "mean large diameter" is based on ten of the largest corallites that were arbitrarily selected in the transverse thin section(s) of a given colony. "Maximum diameter" is a measure of the largest corallite found in the same section(s).

FAVOSITES ("EMMONSIA") EMMONSII Hall, 1877

Plate 1, figures A-D

?*Favosites Emmonsii* ROMINGER, 1876, p. 27, 28, Pl. 7, fig. 1 (upper right on plate), ?Pl. 7, fig. 2.

Favosites Emmonsii HALL, 1877, Pl. 9 explanation, Pl. 12, fig. 5 (other figs. on Pls. 9, 11, 12 are questionable).

Emmonsia emmonsii (Hall). FENTON AND FENTON, 1936, p. 35, 36, Pl. 1, figs. 8-10.

?*Emmonsia emmonsii* (Rominger). SWANN, 1947, p. 260-262, Pl. 7, figs. 4-6, Pl. 7, fig. 1; STUMM, 1964, p. 66, Pl. 63, figs. 1-3 (4?).

Synonymy.—A complete synonymy and description of *Favosites* ("*Emmonsia*") *emmonsii* is beyond the scope of this paper. The citations above include four papers basic to the Hall-Rominger question. In addition, Swann (1947) published the first adequate photographs of *F.* ("E.") *emmonsii*-like squamulae from a specimen from the Columbus Limestone (Ohio, Eifelian). The same illustrations were reproduced by Stumm (1949, card 199).

Description of Hall's lectotype.—Massive, lenticular colony; preserved fragment is 5.0 cm high and 8.0 and 11.0 cm in width and length, respectively. Corallites up to 2.2 mm in diameter; mean large diameter, 2.1 mm.

Squamulae abundant, tongue-shaped, inclined upward, proximally thickened and smoothly tapering to distal end, commonly extend to axis. Tabulae short and irregular, commonly connect the inner ends of squamulae. In longitudinal sections, the apparently regular transverse partitions are a combination of squamulae that enter the plane of the section from different directions and the less common tabulae; spacing of "partitions" averages ten per 5.0 mm. Mural pores are large and in one to three (rarely four) longitudinal rows.

Discussion.—In addition to the Hall (1877) lectotype (specimen 1; NYSM 6216, designated by Fenton and Fenton, 1936; see Plate 1, figures A-D), the following specimens have been examined that may or may not be conspecific: (2, 3) two topotype specimens (FMNH-UC 35773 and USNM 449102, reef facies of the Edgecliff Member, Williamsville, western New York); (4) one specimen from Edgecliff Member reef facies near Ravena, eastern New York (USNM 449103); (5) one specimen from the basal Edgecliff sandstone in the Seneca Stone Corp. quarry (USNM 449104, Plate 2, figures A-E); (6-8) three specimens from the Edgecliff non-reef facies near Cobleskill, east-central New York (USNM 449105-449107; one is shown on Plate 3, figures E-F); (9) one specimen from the lower part of the Oriskany Sandstone at O'Hara's Woods (USNM 44910B, Plate 3, figures A-D); and (10) the Rominger lectotype from near Louisville, Kentucky (UMMP 8449, designated by Stumm, 1964; Plate 1, figures E-F). The overall similarity of all of these specimens is striking; the ten specimens show considerable variation, but this seems to be within the limits of a single species. However, there is a need for restudy of "populations" from the Edgecliff Member in western New York and the Jeffersonville Limestone in the vicinity of the Falls of the Ohio to determine the scope of the Hall and Rominger "species" before they, and the other forms described herein, can be either synonymized or distinguished with confidence.

The three non-reef Edgecliff specimens (6-8, above) and the Edgecliff sandstone specimen (5, above) are similar to Hall's lectotype in most respects but have smaller corallites (mean large diameters from 1.7-1.9 mm) and vertically striated walls (see description and illustrations of *Favosites* ("*Emmonsia*") sp. 1 cf. *F.* ("E.") *emmonsii*). The lack of this wall structure in the other specimens may be due to poorer or different preservation, but this possibility is not convincing because

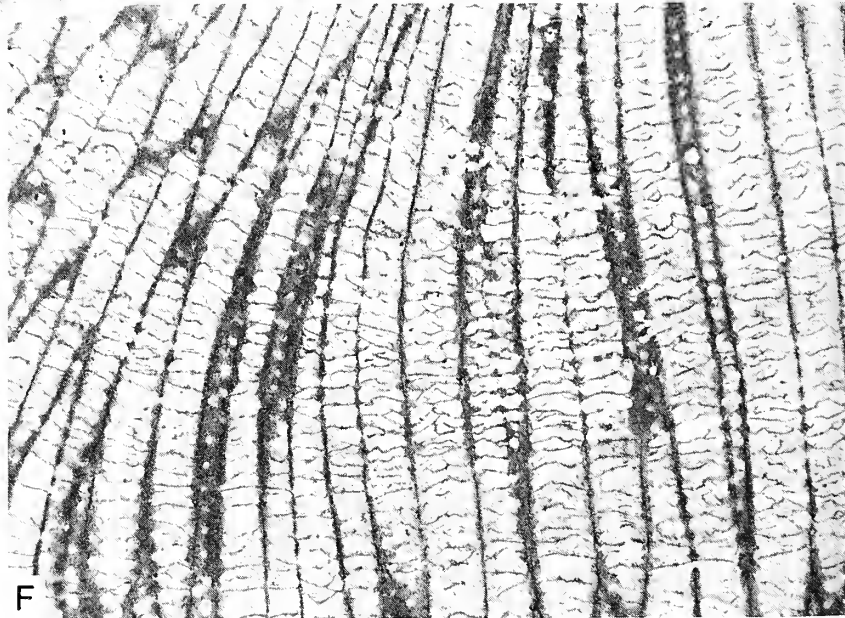
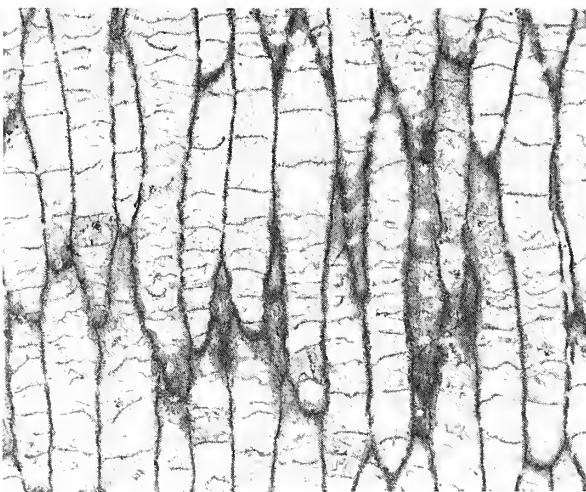
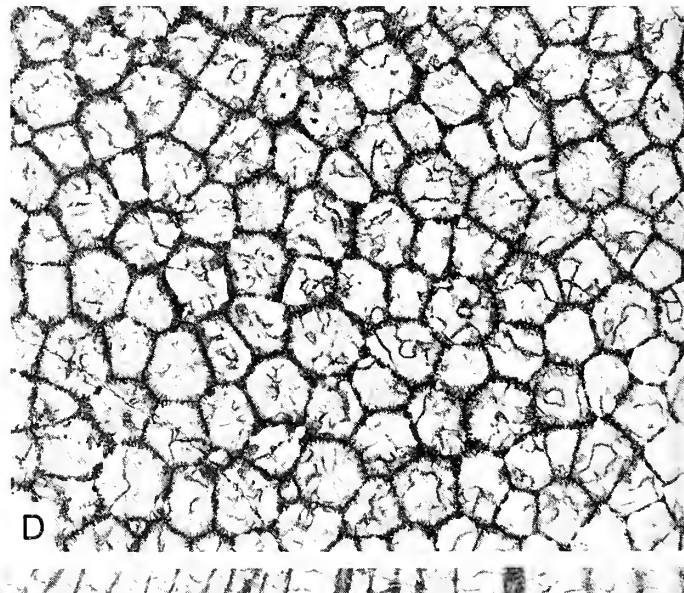
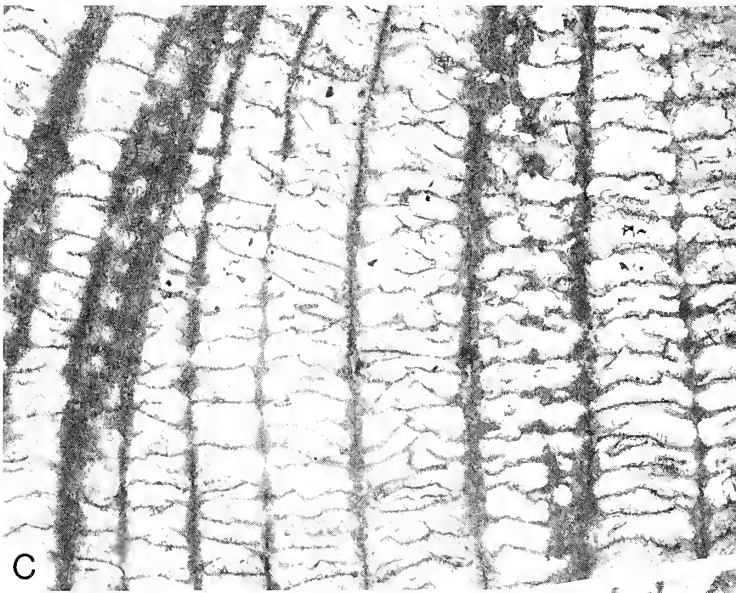
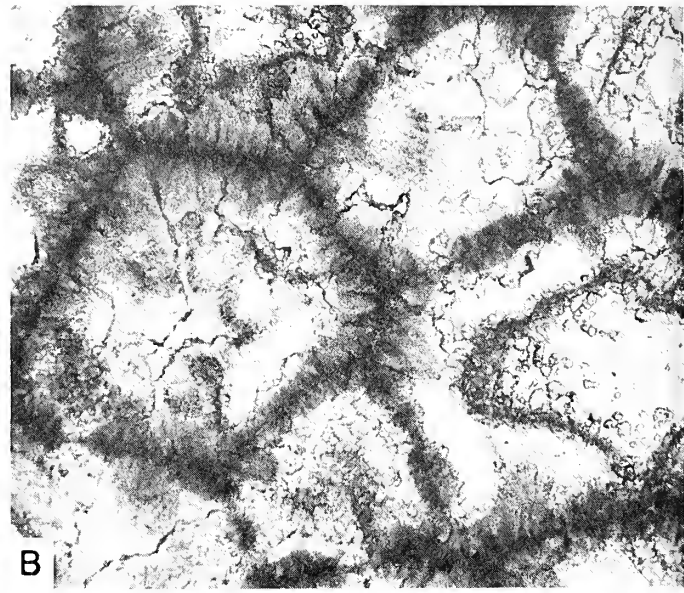
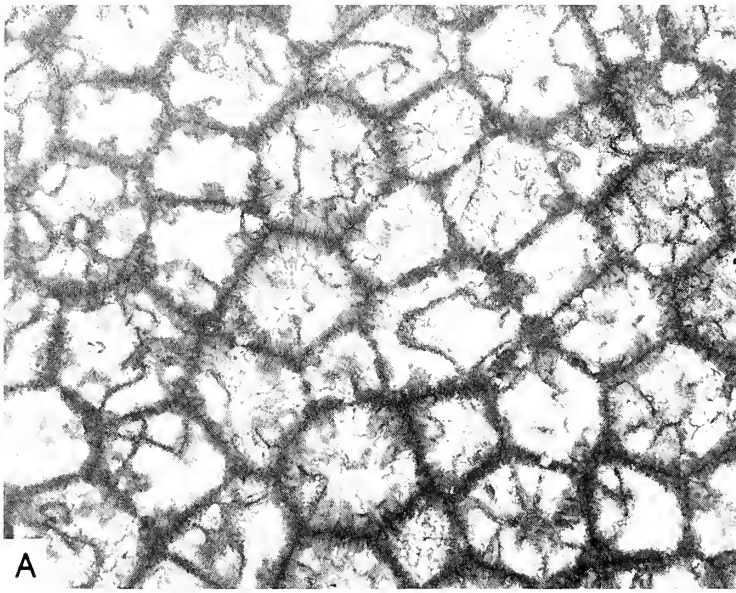


Plate 4. *Favosites* ("Emmonsia") *alternata* n. sp. A-F, Holotype (form A), USNM 449109, lower Oriskany Sandstone, Seneca Stone Corp. quarry, USGS collection 10324-SD; transverse and longitudinal thin sections, x10, x25, x10, x5, x5, x5, respectively; E and F illustrate different longitudinal sections of the same colony, C and D illustrate the same section.

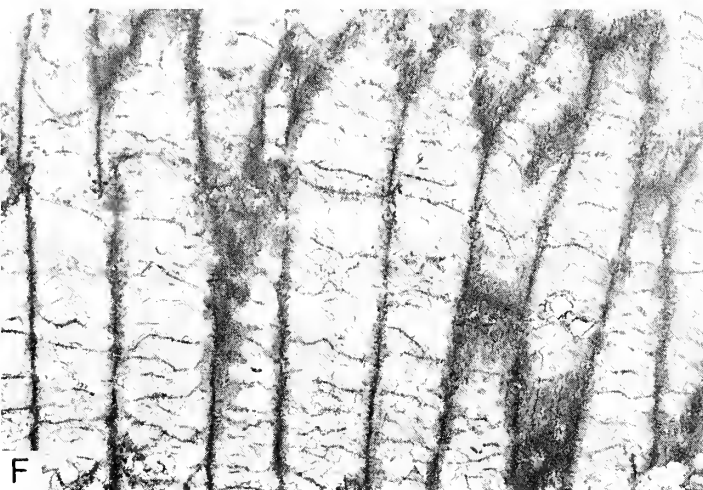
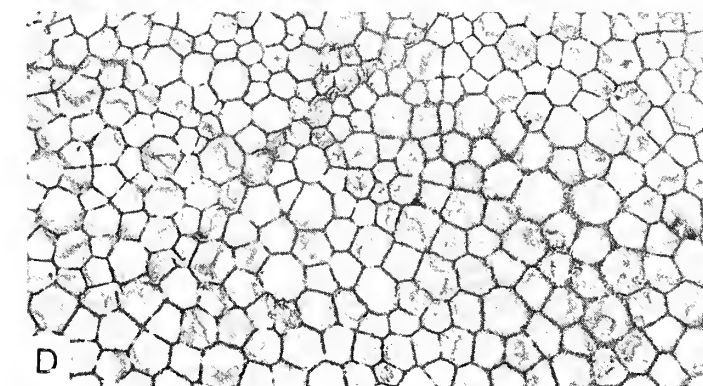
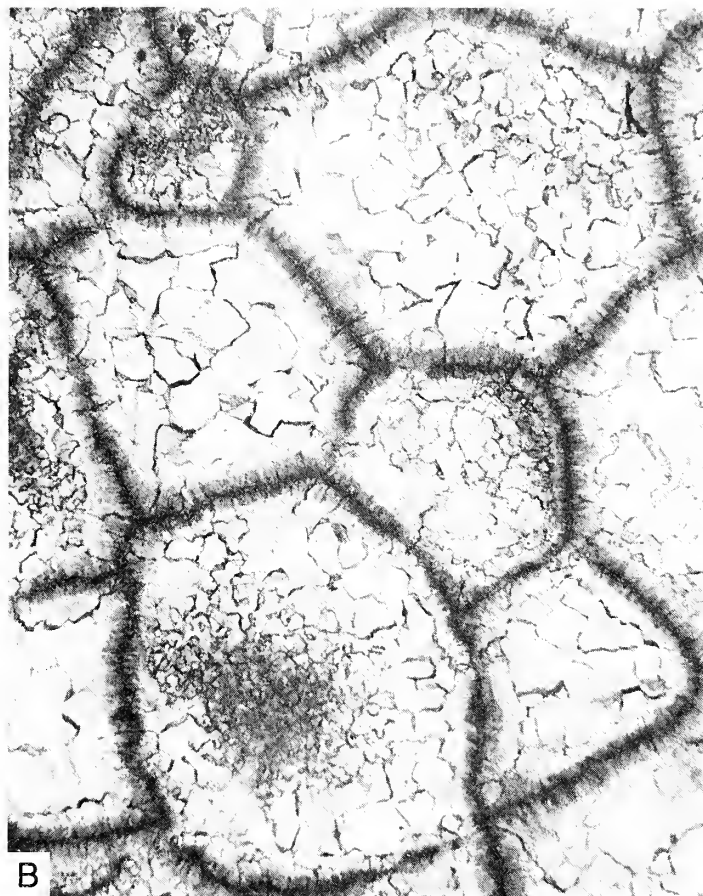
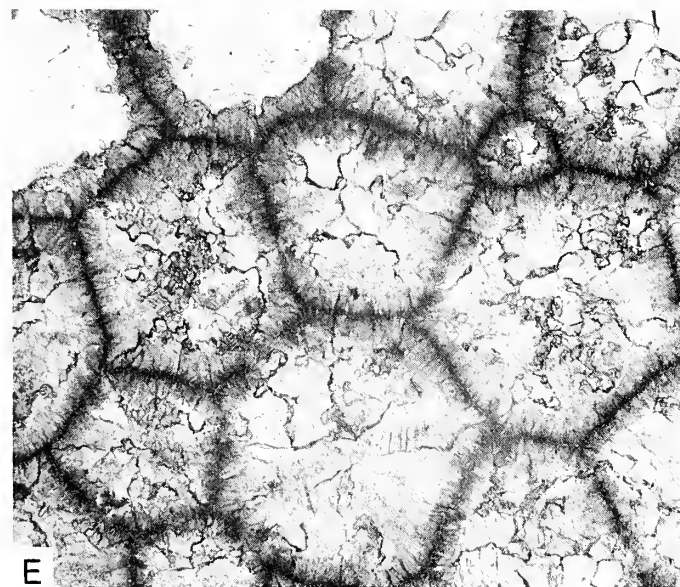
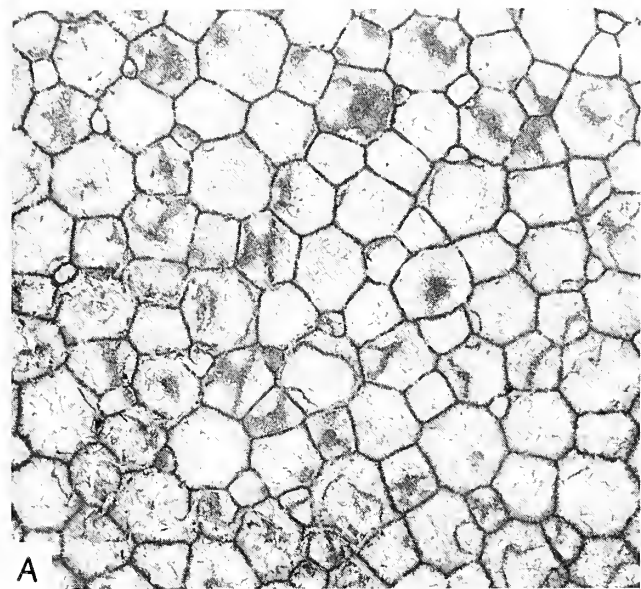


Plate 5. *Favosites* ("Emmonsia") *alternata* n. sp. A-C, Form A, paratype, USNM 449110, lower part of the Oriskany Sandstone, Seneca Stone Corp. quarry, USGS collection 10324-SD; transverse and longitudinal thin sections, x5, x25, x5, respectively. D-F, Form B, paratype, USNM 449117, lower Oriskany Sandstone, Yawger's Woods, USGS collection 10435-SD, transverse and longitudinal thin sections, x5, x25, x10, respectively.

the preservation of all the other Edgecliff specimens is otherwise similar and the structure is striking. It may be significant that the non-reef Edgecliff colonies in this small sample have striate walls, whereas reef facies colonies do not.

The Rominger lectotype (1876) also lacks the wall structure. It differs from the Hall (1877) lectotype in its smaller corallite size (mean large diameter=1.8 mm), finer squamulae, and smaller(?) pores.

The single Oriskany specimen has the smallest corallites of any in the group. It lacks the wall striations and differs in other ways that may or may not be important (see description).

The significance of the striated wall structure is not known. It is one of the many questions that must be answered before "*Emmonsia*" can be fully understood.

FAVOSITES ("EMMONSIA") SP. 1 CF. F. ("E.") EMMONSII

Hall, 1877

Plate 2; Plate 3, figures E-F

Onondaga specimen.—A single colony from the basal sandy beds of the Edgecliff Member in the Seneca Stone Corp. quarry is thought to be conspecific with colonies from the non-reef Edgecliff at Cobleskill, east-central New York. The four specimens may belong to Hall's species.

Diagnosis.—*Favosites* known from massive colonies with corallites up to 2.0 mm or more in diameter. Squamulae long and abundant, thickened, angulate, commonly joined by irregular tabulae suspended from their inner ends. Walls composed of longitudinal units of uncertain origin; pores in one or more rows.

Description.—The colony from the Edgecliff sandstone is broadly lenticular in form, with a maximum preserved height of 16 mm, which tapers to 2.0 mm in a distance of 8.0 cm; the maximum preserved diameter is 12 cm. The colony is not complete, and the original dimensions may have been significantly greater. The three limestone colonies are fragments with maximum preserved heights and diameters of approximately 8.0 cm.

Corallites up to 1.8 to 2.1 mm diameter; mean large diameter 1.7-1.9 mm. Squamulae long and irregularly angulate in shape, concave along the short axis, inclined upwards toward the calice; moderately but uniformly thickened; in distinct longitudinal rows. Tabulae short, thin, concave or irregular; commonly suspended from the squamulae and connect their inner ends at irregular angles. In longitudinal sections, the apparent transverse partitions are a complex of squamulae, which enter the plane of the section from all directions, and the less-common tabulae. The mural pores are large and in one to three rows.

Corallite walls are composed of longitudinal units that give a striated appearance in vertical sections (Plate 2, figures D, E). In transverse sections, these are seen as radiating units that extend from the dark center lines of the walls into the lighter-colored inner wall, where the unit boundaries fade into featureless, light-colored walls or squamulae. The wall units are less than 0.08 mm wide (measured parallel to the wall in either transverse or vertical section). Squamulae (measured parallel to end just inside the wall) are 2.0 to 4.0 mm wide; in transverse sections, the boundaries of the squamulae correspond to unit boundaries; four to six units commonly form the base of each squamula.

Discussion.—The Seneca Stone Corp. quarry specimen of *Favosites* ("*Emmonsia*") sp. 1 cf. *F. ("E.") emmonsii* was collected in a loose block of medium to medium dark grey sandy limestone and is from the bed of reworked "Oriskany" sand in the base of the unconformably overlying Edgecliff Member of the Onondaga Limestone. Disarticulated brachiopod valves (small and unlike those found in the

Oriskany Sandstone), pelmatozoan stem plates, and "phosphate" nodules are in the same block. The coral colony could not have been transported far without breaking up, and it is assumed that it grew in the agitated environment suggested by the lithology. Similar beds of reworked sand with Onondaga fossils are known at many outcrops in the area. The three supplementary specimens are from the more characteristic limestone facies of the Edgecliff Member in a small exposure at Cobleskill, New York.

Favosites ("*Emmonsia*") sp. 1 cf. *F. ("E.") emmonsii* is compared with *F. ("E.") emmonsii* and the Oriskany *F. ("E.")* spp. in the discussions of those species. The significance of the "striated" wall is unclear. The structure is known in other favositids, although not common; to some extent, it may be a function of preservation in the Edgecliff specimens. However, no reason is apparent why these four specimens from such different lithologies should have this structure, whereas the other possible *F. ("E.") emmonsii* do not.

Material.—USNM 449104, USGS collection 10436, basal sandy beds of the Edgecliff Member of the Onondaga Limestone, late Emsian or early Eifelian, Seneca Stone Corp. quarry, USNM 449105-449107, Edgecliff Member, Cobleskill, New York.

FAVOSITES ("EMMONSIA") SP. 2 CF. F. ("E.") EMMONSII

Hall, 1877

Plate 3, figures A-D

Oriskany specimen.—A single large colony was sampled from the lower Oriskany Sandstone at O'Hara's Woods. In the outcrop, the colony is in growth position (Figures 2, 5).

Description.—The colony is 20 cm high and 60 cm wide. A sample from the upper part of the colony has corallites up to 1.6 mm in diameter with a mean large diameter of 1.5 mm. Walls thick. Squamulae abundant, thickened at the corallite wall but generally thin, long, commonly inclined upwards and extend to, or nearly to, the axis. Tabulae complete or incomplete and suspended from the squamulae. Mural pores in one or two rows.

Discussion.—*Favosites* ("*Emmonsia*") sp. 2 cf. *F. ("E.") emmonsii* is similar to *F. ("E.") emmonsii* and may be conspecific with one or more of the specimens described or discussed above as *F. ("E.") emmonsii* or *F. ("E.")* sp. cf. *F. ("E.") emmonsii*. It differs from the Hall (1877) lectotype and the other Edgecliff specimens in its small corallites, thin squamulae, thick wall, and more common complete tabulae; it differs from the Edgecliff sandstone and limestone specimens in lacking the striated wall.

Material.—USNM 449108, lower Oriskany Sandstone, Pragian age, O'Hara's Woods.

FAVOSITES ("EMMONSIA") ALTERNATA n. sp.

Plates 4-7

Diagnosis.—*Favosites* species with lenticular, globose, or irregular colonies up to 12 cm or more in height, 40 cm or more in diameter; mean large diameter of corallites varies from 1.1-2.1 mm. Short, attenuated squamulae abundant in zones that tend to alternate with squamulae-free zones of thin tabulae. Mural pores numerous.

Discussion.—Two forms are recognized primarily on the basis of size and have additional character differences that may or may not be significant. These are described separately because it is thought that larger samples may show them to be distinct species. Both forms occur in the lower 27 cm of the Oriskany Sandstone at the Seneca Stone Corp. quarry. Form B also occurs in the lower Oriskany at Yawger's Woods.

Material.—Holotype, USNM 449109, form A, USGS collection

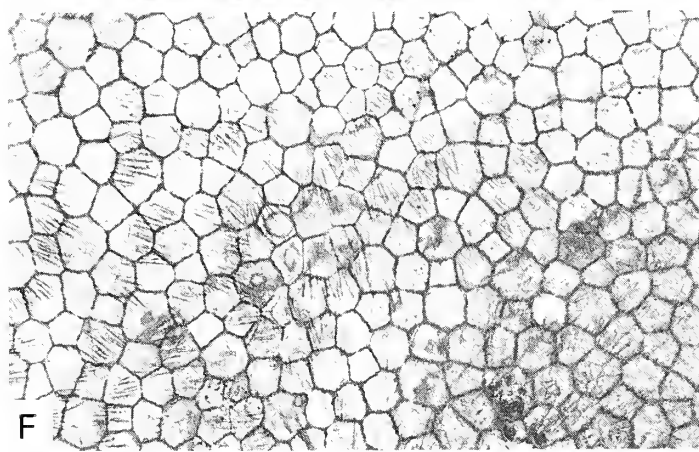
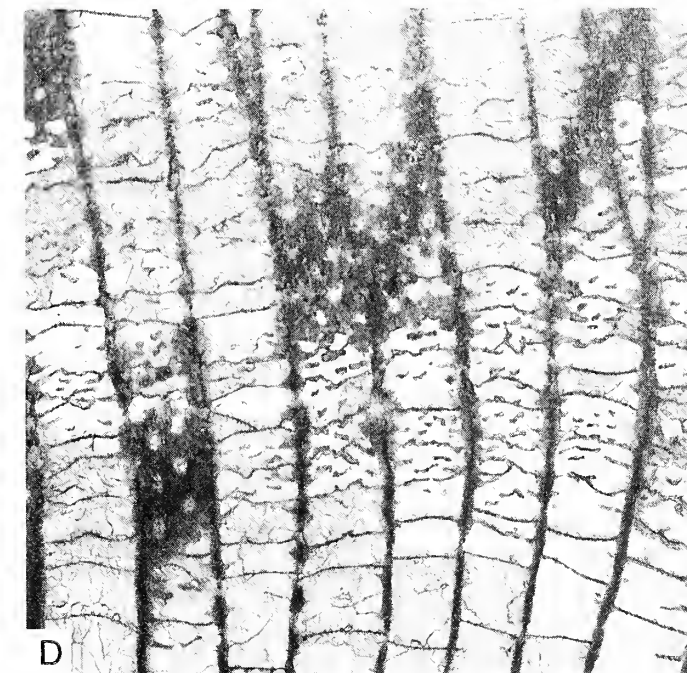
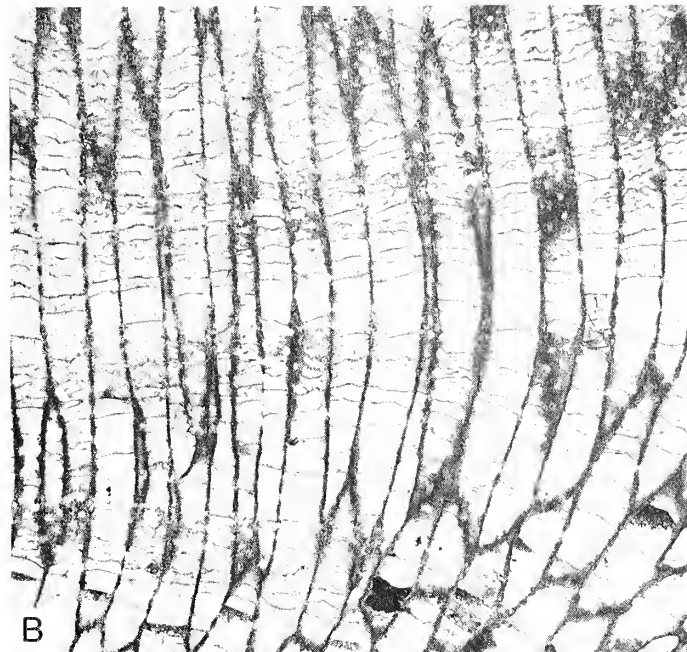
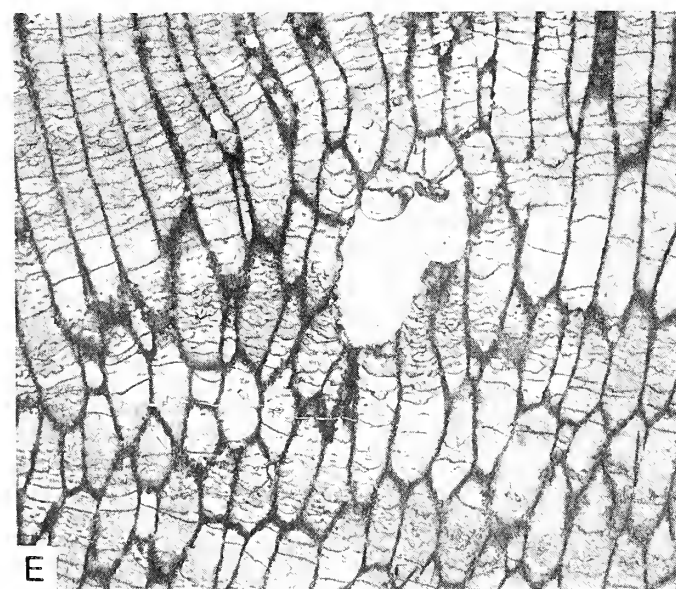
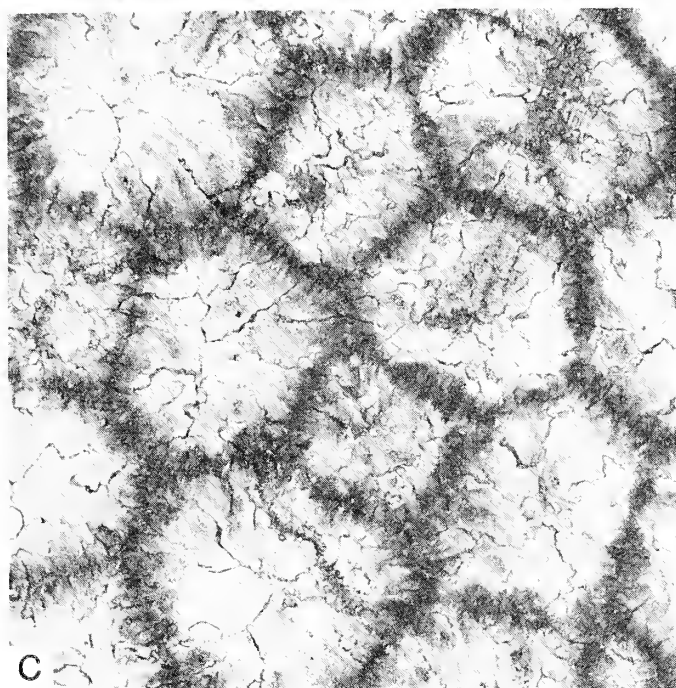
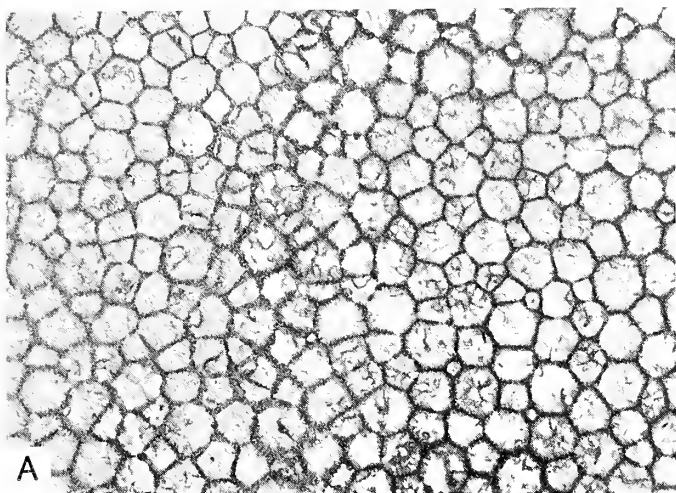
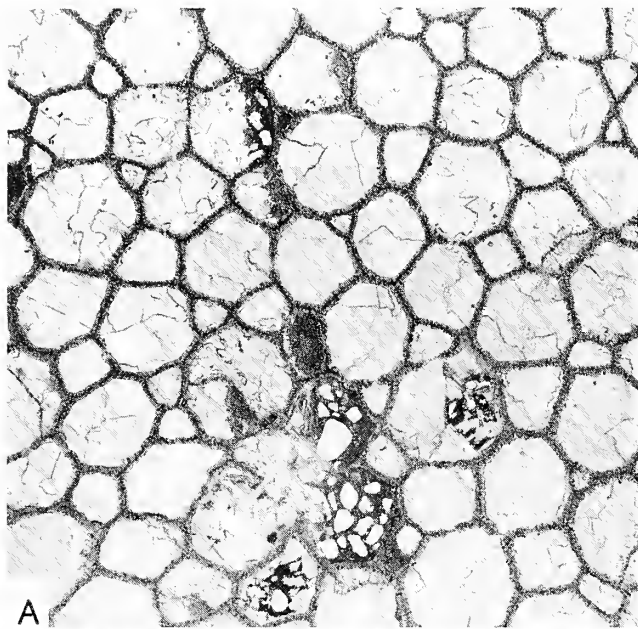
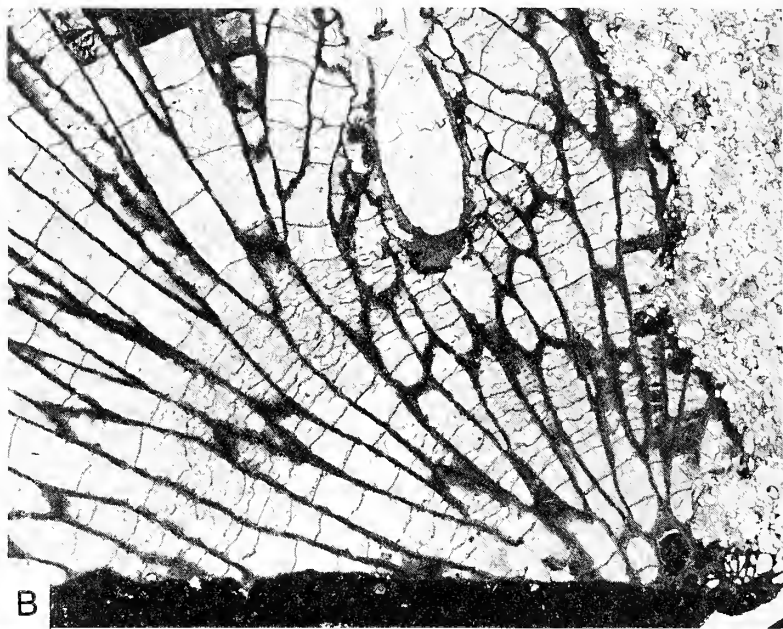


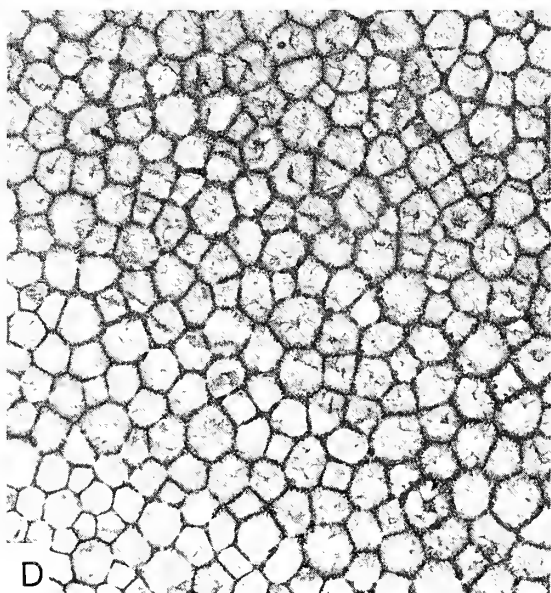
Plate 6. *Favosites* ("Emmonsia") *alternata* n. sp. form B; lower part of the Oriskany Sandstone, Seneca Stone Corp. quarry, USGS collection 10324-SD. A-D, Paratype, USNM 449114, transverse and longitudinal thin sections, x5, x5, x25, x10. E-F, Paratype, USNM 449115, longitudinal and transverse thin sections, x5.



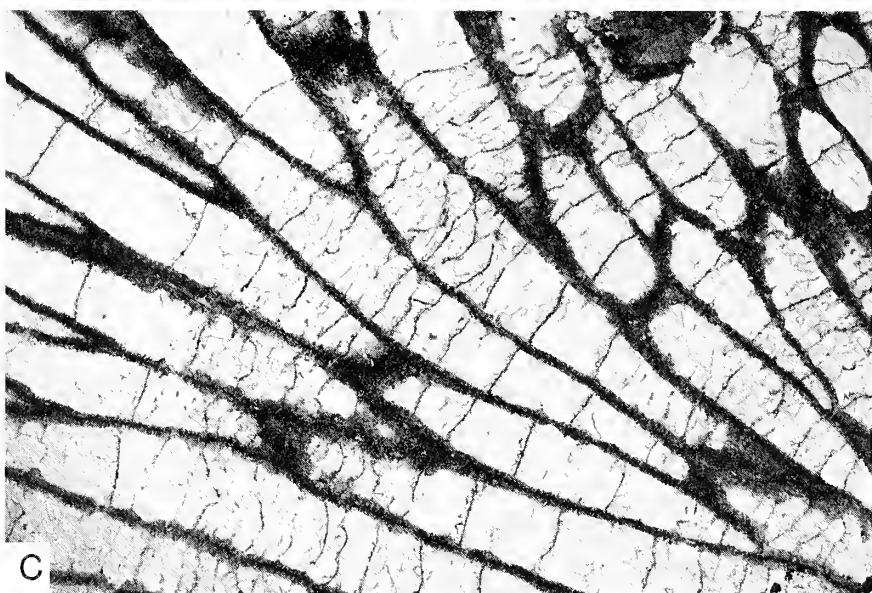
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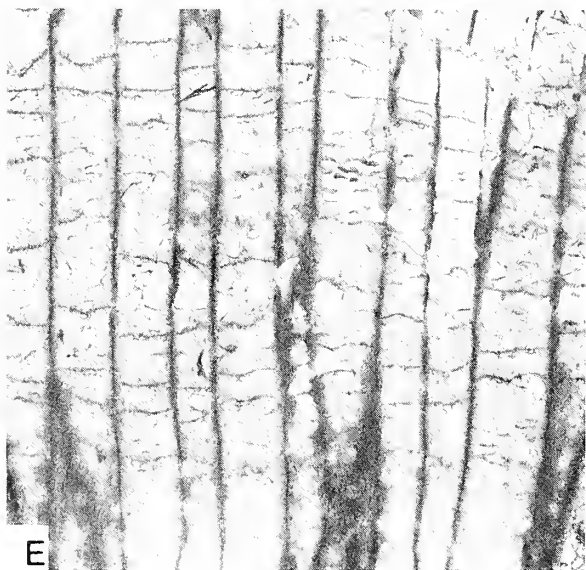
B



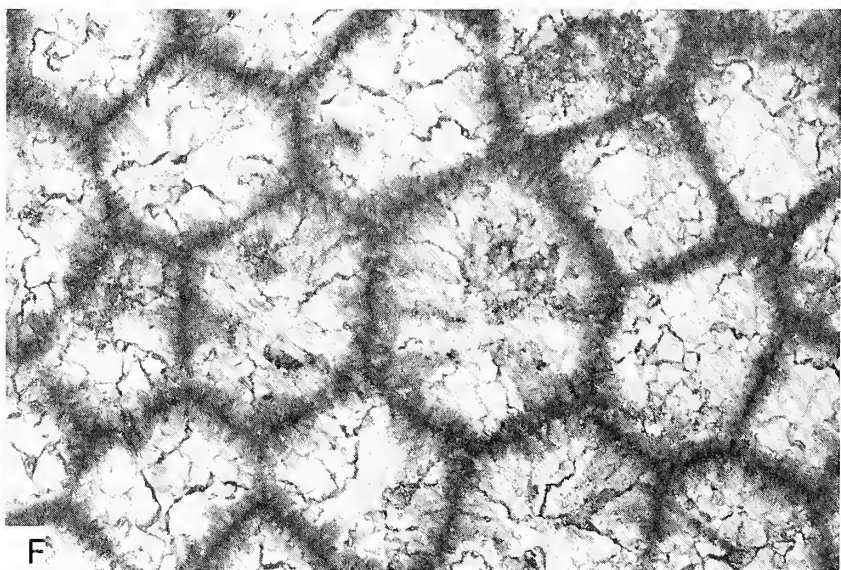
D



C



E



F

10324, lower part of the Oriskany Sandstone, Pragian age, Seneca Stone Corp. quarry. Nine paratypes, USNM 449110-449118; see descriptions of the two forms for details.

FAVOSITES ("EMMONSIA") ALTERNATA n. sp. FORM A
Plate 4; Plate 5, figures A-C

Diagnosis.—Form of *Favosites* ("*Emmonsia*") *alternata* n. sp. with globose, knobby, irregular colonies up to 12 cm or more in height and 24 cm or more in diameter; corallites up to 2.3 mm diameter. Attenuated squamulae abundant in zones that alternate with squamula-free zones of thin tabulae. Mural pores numerous.

Description.—Portions of two large colonies are 10 and 12 cm high and 24 and 20 cm in maximum known diameter; both exhibit irregular growth that led to knobby globose coralla; three additional specimens are fragments of globose coralla of unknown size.

Corallites up to 1.8 to 2.3 mm diameter (in the five colonies); mean large diameter varies from 1.7 to 2.0 mm. Squamulae relatively thin and short, tend to occur in zones. Zones of abundant squamulae and closely spaced, irregular, incomplete or complete tabulae alternate with zones of complete, widely spaced tabulae; the tabulae are thin. Walls apparently non-striate. Mural pores large, in one or two longitudinal rows; no relationship is evident between the positions of squamulae and pores.

Discussion.—*Favosites* ("*Emmonsia*") *alternata* n. sp. form A occurs in the lower part of the sandstone along with *F. ("E.") alternata* n. sp. form B and scattered, disarticulated, large brachiopod valves. None of the corals are known to be in living position, and some are overturned. However, it seems unlikely that either the corals or the brachiopods were transported very far because of the excellent preservation of reasonably complete specimens.

Favosites ("*Emmonsia*") *alternata* n. sp. form A differs from form B in its larger corallite size, in the apparent lack of wall striations, and in the different relative thicknesses of the alternating squamulate and non-squamulate zones. It differs from *F. ("E.") congesta* n. sp. and *F. ("E.") emmonsii* in its thin, small squamulae.

Material.—Species holotype, USNM 449109; illustrated paratype, USNM 449110; two unillustrated paratypes, USNM 449111, 449112; USGS collection 10324-SD, lower Oriskany Sandstone, Pragian age, Seneca Stone Corp. quarry. One unillustrated paratype, USNM 449113, was collected loose from the same locality and probably is from the same stratigraphic position.

FAVOSITES ("EMMONSIA") ALTERNATA n. sp. FORM B
Plate 5, figures D-F; Plates 6-7

Diagnosis.—Lenticular or globose, irregular colonies up to 12 cm in height and 40 cm or more in diameter; corallites up to 1.4 mm diameter. Zones with abundant attenuated squamulae alternate with generally thinner zones with few squamulae. Walls composed of longitudinal units; mural pores numerous.

Description.—Portion of large, lenticular colony has a maximum height of 4 cm that tapers to 1.5 cm and incomplete diameters of 13 and

7 cm. A second colony is nearly spherical, 2.5 cm in diameter, and grew attached to a flat pebble derived from the underlying Manlius Limestone. Three additional specimens are incomplete, but the largest indicates an irregular, massive growth form (Plate 5) with height and diameter in excess of 20 and 40 cm.

Corallites up to 1.3 to 1.4 cm in diameter (in five colonies); near large diameter varies from 1.1-1.4 mm. Squamulae relatively thin and short, tend to occur in zones. Thicker zones of abundant squamulae and closely spaced, irregular tabulae alternate with commonly thinner zones of complete, widely spaced tabulae; all tabulae are thin. Corallite walls are composed of longitudinal units similar to those described in *Favosites* ("*Emmonsia*") sp. 1 cf. *F. ("E.") emmonsii*; wall units are seen in both longitudinal and transverse sections. Mural pores large, commonly in two longitudinal rows; no relationship is evident between the positions of squamulae and pores.

Discussion.—*Favosites* ("*Emmonsia*") *alternata* n. sp. form B occurs in the lower half of the Oriskany Sandstone with *F. ("E.") alternata* n. sp. form A and scattered disarticulated large brachiopod valves. The small spherical colony is preserved in living position, and the large, lenticular colony is probably right side up; neither the corals nor the brachiopods are thought to have been transported very far because of the generally excellent preservation.

Favosites ("*Emmonsia*") *alternata* n. sp. form B differs from form A in its small corallite size and striate walls (apparently lacking in form A) and in having thicker squamulate than non-squamulate zones. It differs from *F. ("E.") congesta* n. sp. and *F. ("E.") emmonsii* in its thin, relatively short squamulae.

Material.—Five illustrated paratypes, USNM 449114-449116, USGS collection 10324-SD, Seneca Stone Corp. quarry; USNM 449117 and 449118, USGS collection 10435-SD, Yawger's Woods. Lower Oriskany Sandstone, Pragian age.

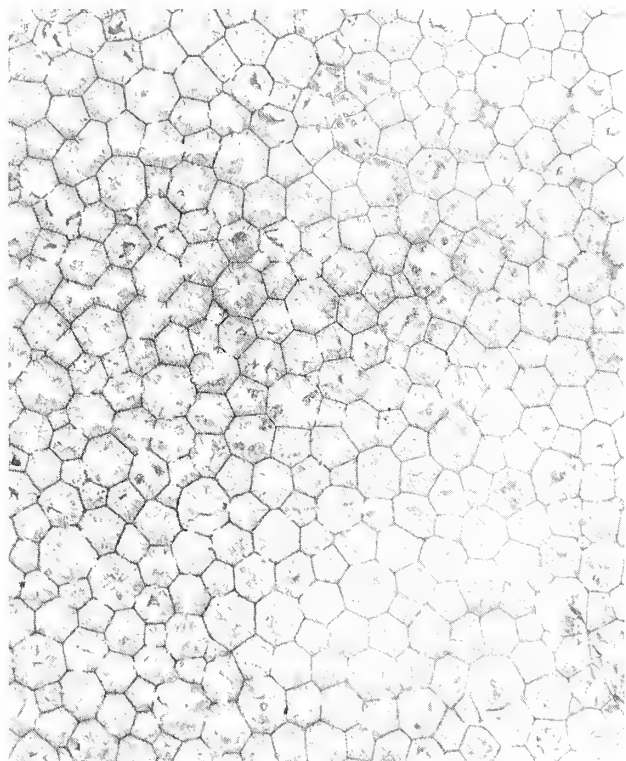
FAVOSITES ("EMMONSIA") CONGESTA n. sp.
Plates 8, 9

Diagnosis.—*Favosites* species with massive colonies; corallites up to 1.5 mm diameter. Thickened squamulae abundant, may almost fill the lumen in transverse sections or be locally absent. Mural pores numerous.

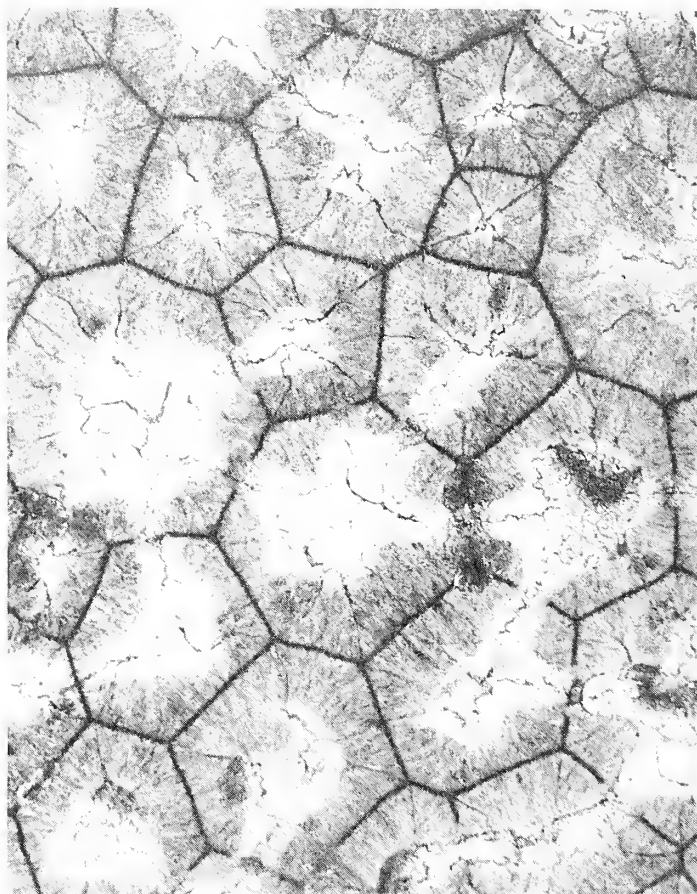
Description.—Massive coralla of unknown shape and size. Five studied specimens are fragments of larger colonies; maximum known height 4 cm; maximum known diameter 8 cm.

Corallites up to 1.2 to 1.5 mm diameter (in the five specimens); mean large diameter varies from 1.1 to 1.4 mm. Squamulae thick, medium-long and blunt; commonly extend almost to the corallite axis and nearly fill the lumen; locally, the squamulae are thin or lacking. Tabulae complete or incomplete and suspended from the squamulae; thickened on upper surfaces where squamulae are thick, but attenuate where squamulae are thin; spacing irregular but commonly approximates the corallite diameter. There is little suggestion of zonation; the variation from thick to thin squamulae and tabulae takes place both horizontally and

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Plate 7. *Favosites* ("*Emmonsia*") *alternata* n. sp. form B. A-C, Paratype, USNM 449116, lower part of the Oriskany Sandstone, Seneca Stone Corp. quarry, USGS collection 10324-SD; transverse and longitudinal thin sections, x10, x5, x10, respectively; B shows the coral grown over a fragment of the Manlius Limestone (lowest part of figure) that was reworked into the lower Oriskany Sandstone. D-F, Paratype, USNM 449118, lower Oriskany Sandstone, Yawger's Woods, USGS collection 10435-SD; transverse and longitudinal thin sections, x5, x10, x25, respectively.



A



B



C



D

Plate 8. *Favosites* ("Emmonsia") *congesta* n. sp. A-D. Holotype, USNM 449119, upper part of the Oriskany Sandstone, Seneca Stone Corp. quarry, USGS collection 10323-SD; transverse and longitudinal thin sections, x5, x25, x5, x10, respectively.

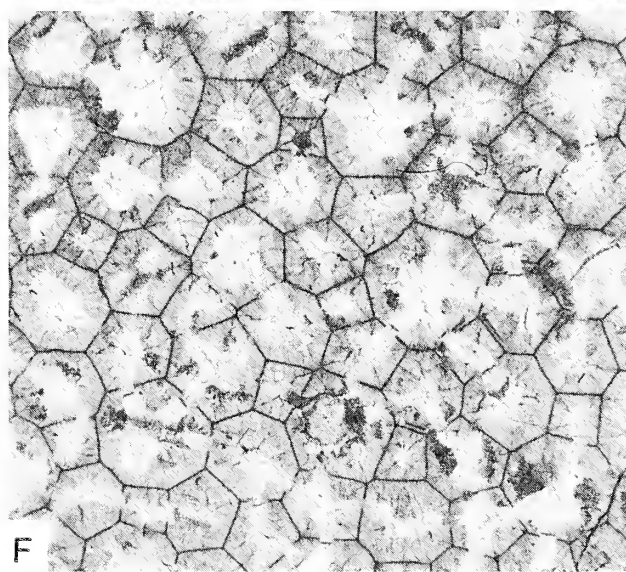
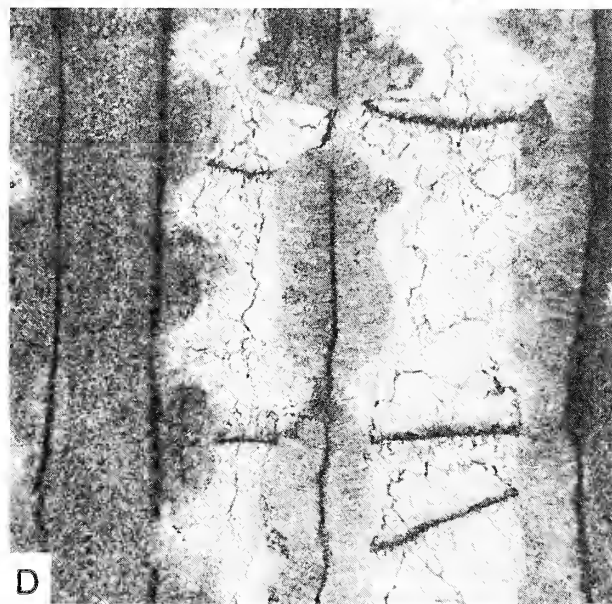
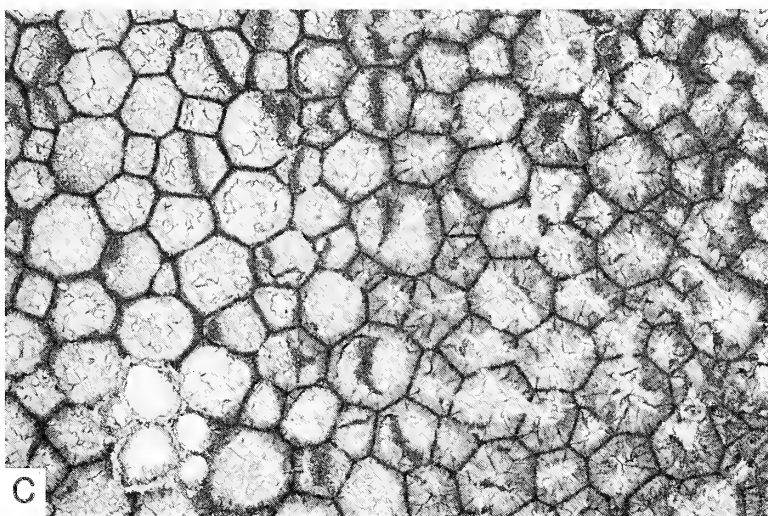
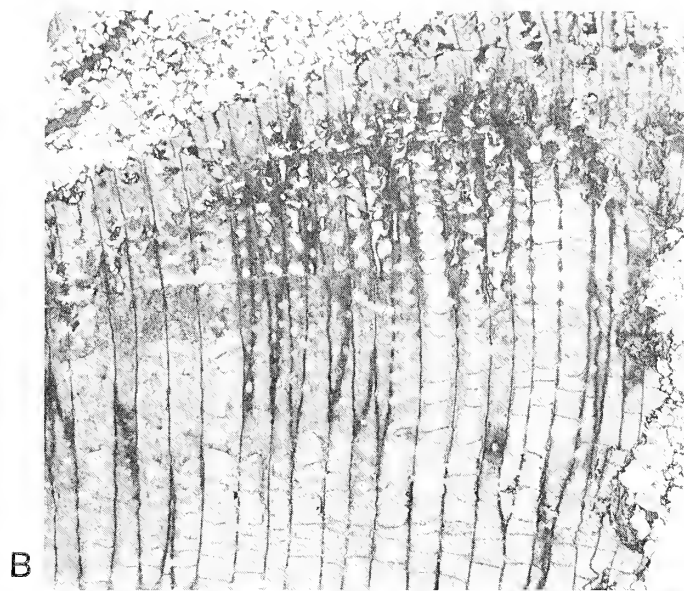
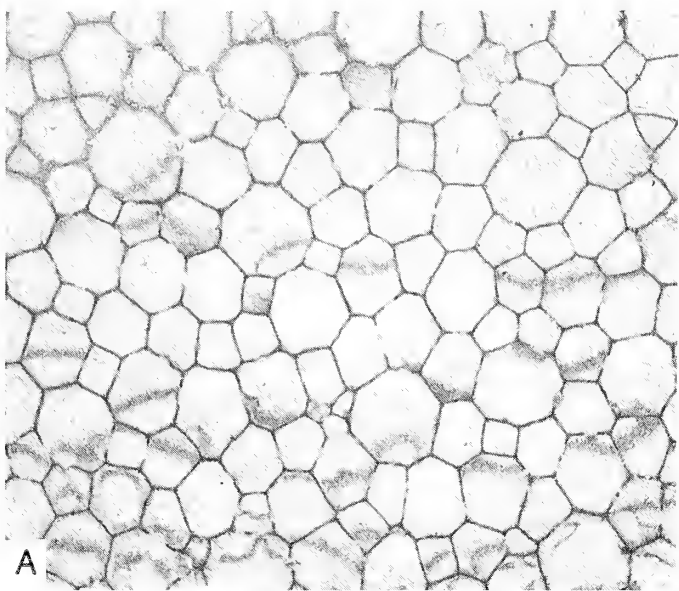


Plate 9. *Favosites* ("Emmonsia") *congesta* n. sp.; upper part of the Oriskany Sandstone, Seneca Stone Corp. quarry, USGS collection 10323-SD. A-C, Paratype, USNM 449120, transverse and longitudinal thin sections, x10, x5, x10, respectively. D-F, Paratype, USNM 449121; longitudinal and transverse thin sections, x10, x5, x10, respectively. D-F, Paratype, USNM 449121; longitudinal and transverse thin sections, x25, x10, x10, respectively.

vertically within the coralla. Mural pores large, in one or two longitudinal rows.

Discussion.—*Favosites* ("Emmonsia") *congesta* n. sp. occurs in the upper 15 cm of the Oriskany Sandstone in the "big-shell" bed in the Seneca Stone Corp. quarry. None of the corals is complete, and the brachiopod shells are disarticulated. However, the preservation of the coral microstructure and of the individual shells is good, and the bed is interpreted as a lag accumulation of skeletal parts of animals that lived in the sandy environment.

Favosites ("Emmonsia") *congesta* n. sp. differs from *F.* ("E.") *alternata* n. sp. in its thickened squamulae and tabulae. It differs from *F.* ("E.") *emmonsii* in the blunt, rounded form of its squamulae and the wide spacing of its tabulae.

Material.—Five specimens; holotype, USNM 449119; two illustrated paratypes, USNM 449120, 449121; two unillustrated paratypes, USNM 449122, 449123. USGS collection 10323-SD, upper part of the Oriskany Sandstone, Pragian age, Seneca Stone Corp. quarry.

Dedication

We appreciate the invitation by E. Landing to join in the celebration of Don Fisher's long service and numerous contributions to the paleontology and stratigraphy of New York. The senior author remembers the thirty-five years of friendship and the innumerable, always pleasant, and profitable field conferences and other visits with Don that punctuated those years.

Acknowledgments

The presence of well-preserved favositids at the Seneca Stone Corp. quarry was brought to WSH's attention in 1980 by W.R. Brice; WSH discussed the occurrence with WAO late that year and sent specimens and photographs of the occurrence during January 1981. At almost the same time, the occurrence was noted by D.L. Waters, then a graduate student at Cornell University; he gave the information and some specimens to J.W. Wells, who sent both to WAO in March 1981. In May 1981, WSH, WAO, Waters, and Wells met at the locality, discussed the occurrence, and made the collections that are the basis of this paper. We are indebted to Brice, Waters, and Wells for their help and for sharing their information.

The Seneca Stone Corp., Fayette, New York, and Ted O'Hara and W.W. Patterson, Jr., both of Auburn, New York, kindly allowed us to collect on their properties; we appreciate their cooperation.

Thin-section photographs are by K. Moore; field photos are by WSH. Drafts of the typescript were read by J.M. Berdan and J.T. Dutro, Jr.; we thank them for their helpful reviews.

Specimens for comparison with the Oriskany favositids were lent to us by G.R. Gunnell, Museum of Paleontology, University of Michigan (UMMP); M. Hinkley, American Museum of Natural History (AMNH); E. Landing, New York State Museum (NYSM); and M.H. Nitecki, Field Museum of Natural History (FMNH). Additional abbreviations are for the U.S. National Museum of Natural History, Washington (USNM) and U.S. Geological Survey (USGS). WAO personally supplied \$100 toward publication of this report.

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Appendix: Descriptions of localities

All map references are to USGS 7 1/2-minute topographic quadrangles. Distance measurements in km are from nearest N-S and E-W edges of map. The Oriskany Sandstone localities are described from west to east along the outcrop belt; the straight line distance from first to last is approximately 15 km. The Cobleskill locality is the source of the supplementary collection from the Edgecliff Member.

Seneca Stone Corporation Quarry (formerly Warren Brothers Quarry)

Seneca Co., Romulus 7 1/2-minute Quadrangle. Active limestone quarry, 2.8 km W of east edge, and 2.2 km S of north edge of map. Exposed section extends from the upper part of the Manlius Limestone (approx. 1.5 m exposed) through the Oriskany Sandstone (0-0.6 m; Figures 3, 4) and Onondaga Limestone (25 m) into the lower part of the Marcellus Shale (Union Springs and Cherry Valley Members). The pertinent part of the section is given in the section on local stratigraphy. This is the principal locality for the favositid corals described herein. Access to the quarry was readily granted by the management; anyone seeking to enter the quarry should first obtain permission.

The Oriskany Sandstone is exposed in a test pit in the central part of the quarry. The 0.6 m Oriskany face extends some 10 m laterally, but

the top surface has been cleared over a sizeable area. USGS collection 10324-SD is from the lower 27 cm of the Oriskany Sandstone in the 0.6 m face. USGS collection 10323-SD is from the upper part of the upper 30 cm "big-shell" bed in the face and over the broad surface exposure. USGS collection 10436-SD, including one favositid colony, is from the basal 10 cm of the Edgecliff Member of the Onondaga Limestone; the specimen was collected in a loose block, but is associated with phosphate nodules, abundant quartz sand, and Edgecliff-type fossils. In this area, such a combination is unique to the basal part of the Edgecliff; in the Seneca Stone Corp. quarry, it is found wherever the base of the Edgecliff is exposed, whether or not the Oriskany is present.

The Oriskany Sandstone reaches a maximum thickness of 0.6 m but disappears in the quarry 150-180 m to the south of the test pit, and also to the east; it can be traced some 100 m north from the test pit, but the full thickness is not exposed. Where the Oriskany is missing, the basal phosphate nodule-sandstone beds of the Edgecliff Member rest directly on the Manlius Limestone. The top of this phosphatic zone is exposed on parts of the quarry floor, and numerous other corals and shelly fossils can be seen mixed with the sand and nodules.

Yawger's Woods

Cayuga Co., Union Springs 7 1/2-minute Quadrangle. Well-weathered natural outcrop in woods, 4.2 km W of east edge and 0.9 km S of north edge of map. The Oriskany Sandstone, in discontinuous exposures, can be followed north-south for a distance of 640 m. It is a maximum of 1.4 m thick in the central part of the exposure and thins north and south to 0.5 and 0.6 m, respectively. The Edgecliff Member, with basal sandy, phosphate nodule beds, is locally present. The Oriskany Sandstone is deeply weathered, and the calcareous fossils are commonly leached out to leave molds of the brachiopods and other fossils. Corals are rare, even as molds. However, two large specimens of *Favosites* ("*Emmonsia*") *alternata* n. sp. form B were found by WSH in the lower half of the Oriskany Sandstone. Both were weathered and partly leached, but samples were collected that retained the calcitic skeletal structure. These are cited as USGS collection 10435-SD. The original dimensions of one colony were more than 12 cm in height and 40 cm in length.

O'Hara's Woods

Cayuga Co., Cayuga 7 1/2-minute Quadrangle. Well-weathered natural outcrop in woods, 1.3 km W of east edge and 3.4 km N of south edge of map. Outcrop similar to that in Yawger's Woods. The Oriskany Sandstone is 0.6-0.8 m thick and is overlain in places by as much as 1.2 m of Edgecliff Member with the basal sandy, phosphate nodule beds (Figure 2). The Oriskany Sandstone pinches out some 600 m to the north and can be traced the same distance south. Only one coral was found, despite a lengthy search.

A large colony of *Favosites* ("*Emmonsia*") sp. 2 cf. *F.* ("*E.*") *emmonsii* (Plates 2, 3) was found and sampled by WSH. In outcrop, the colony is right side up, 20 cm high and 60 cm wide. A measured section, at the location of the coral, is given below. This is the section shown in Figure 2. The coral colony apparently grew on the clean sand that formed bed a, at least partly during the deposition of the 23 cm brachiopod coquina (bed b).

Edgecliff Member, lower part only; sandy, phosphate nodule beds at base. Oriskany Sandstone: 0.6+ m.

- e. 5-7.5 cm clean quartz sand, few brachiopods.
- d. 7.5 cm brachiopod coquina.

- c. 7.3-9 cm clean quartz sand, scattered brachiopods.
- b. 23.0 cm brachiopod coquina; "*Emmonsia*" colony in lower part.
- a. 16.5 cm clean quartz sand.

Manlius Limestone, uppermost part only.

Cobleskill

Schoharie Co., Cobleskill 7 1/2-minute Quadrangle. Abandoned quarry in woods in east part of village, 1.7 km E of west edge of map. 6-7 m of lower Onondaga Limestone is mostly Edgecliff Member. Three specimens of *Favosites* ("*Emmonsia*") sp. 1 cf. *F.* ("*E.*") *emmonsii* are from the lower 3 m biostromal facies of the Edgecliff in the quarry. Collected in 1953 by WAO.

The Ordovician trilobite genus *Hemiarges* (Lichidae: Trochurinae) from North America and Greenland

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Abstract

Hemiarges paulianus (Clarke) from the Prosser Limestone of Minnesota is redescribed, supplemented with material from the Bobcaygeon and Verulam Formations ("*H. aeolus*") of Ontario, the Kimmswick Limestone of Missouri ("*H. bartoni*"), and the Franklinian of Chaumont, New York. *Hemiarges paulianus* is closely related to the type species *H. wesenbergensis* (Schmidt) from the Rakvere Formation of Estonia, in the strong convexity of the cranidium and glabellar lobes, incomplete S1, and enlarged glabellar tubercles.

Other closely related forms with comparable key features include *H. troedssoni* n. sp. (Cape Calhoun Formation, northern Greenland), *H. turneri* Chatterton and Ludvigsen (lower part of Esbataottine Formation, District of Mackenzie), *H. turneri amicus* n. subsp. (Crown Point Formation of New York), *H. turneri rasettii* Tripp and Evitt (Edinburg Formation of Virginia), and *H. turneri elassouothos* n. subsp. (upper part of Esbataottine Formation, District of Mackenzie).

Hemiarges tuberculatus (Weller) (Franklinian of New Jersey) and *H. balanus* n. sp. (lower part of Whittaker Formation, District of Mackenzie) constitute a group of less-closely related species with enormously enlarged tubercles. *Hemiarges diadyma* n. sp. (lower part of Whittaker Formation), an antithetical species that lacks all enlarged tubercles and has short, circumscribed bullar lobes, is described.

Enlarged glabellar tubercles occur also in *H. memorans* Öpik from the Porkuni Formation (Hirnantian) of Estonia, a more distantly related species that is characterized by complete S1, circumscribed and weakly swollen bullar lobes, and greatly elongated pygidial free points.

A cladogram is proposed that summarizes the relationships of the above taxa on the basis of cranidial characters and tuberculation. The distinctive features of all named species of *Hemiarges* are tabulated.

Introduction

Lichidae form a minor part of the diverse and abundant Middle Ordovician trilobite faunas from Laurentia. *Hemiarges* is the most common lichiid genus in these rocks, and *Hemiarges paulianus* (Clarke, 1894), the earliest described North American species (see Figure 1), has been reported from widely scattered localities from Missouri to Greenland. The type material of this species has never been adequately illustrated, and the only available description is Clarke's (1894). A conspicuous feature of *Hemiarges paulianus* is the enlargement of certain glabellar tubercles, and this report is centered on their systematic

significance, larval homologies, and occurrence in other taxa, several of which are described. Species in which only the primary tubercles on the fixigenae are enlarged are compared. Enlargement of glabellar tubercles culminates in *H. balanus* n. sp.; the antithetical species, *H. diadyma* n. sp., which lacks enlarged tubercles, is described for comparison. The distinctive features of all named species of *Hemiarges* are summarized (Table 1).

Materials and methods

The series of specimens from St. Paul, Minnesota, that Clarke (1894) apparently used to erect *Hemiarges paulianus* are repositied in the U.S. National Museum (USNM). These have been restudied, along with a number of additional specimens from the same area that are also repositied in the USNM. In addition, specimens identified as *H. paulianus* from Ontario have been examined at the Geological Survey of Canada and the Royal Ontario Museum. Plaster casts of *H. paulianus* and *H. warburgae* of Troedsson (1928) from the Cape Calhoun Formation of northern Greenland were made available by Dr. V. Poulsen of the University of Copenhagen. The primary types of *H. tuberculatus* (Weller, 1903); *H. bartoni* Raymond, 1925; *H. leviculus* Bradley, 1930; and *H. aeolus* Sinclair, 1944, have also been studied in order to determine their relationship to *H. paulianus*. Material from the Esbataottine and Whittaker Formations, District of Mackenzie, described herein, was collected by R. Ludvigsen.

Sweet (1988, p. 86, fig. 1) proposed the informal stage designation "Franklinian" and divided it into three substages: Rocklandian, Kirkfieldian and Shermanian. His arguments that the term "Trentonian" should be abandoned are accepted in this report.

Terminology and abbreviations used in this paper are essentially those of Harrington et al. (1959, p. 117-126), with the exception that the glabella is considered to include the occipital ring. Thomas and Holloway (1988, p. 188, fig. 2) adopted Szalay's (1955) terms "L1b" for the main posterior lateral glabellar lobe and "L1a" for the subsidiary posterolateral swellings (formerly regarded as occipital lobes), and Temple's (1972, p. 374) term "bullae" (singular—"bulla") for the anterolateral lobes. These are accepted in this report. The terms "granulation" for the finer grade of prosopon and "tuberculation" for the coarser are used herein. The wide range in cranidial size among the taxa examined herein makes it impossible to define individual prosopon elements in consistent absolute values. It should be noted that larger granules and tubercles are usually perforate.

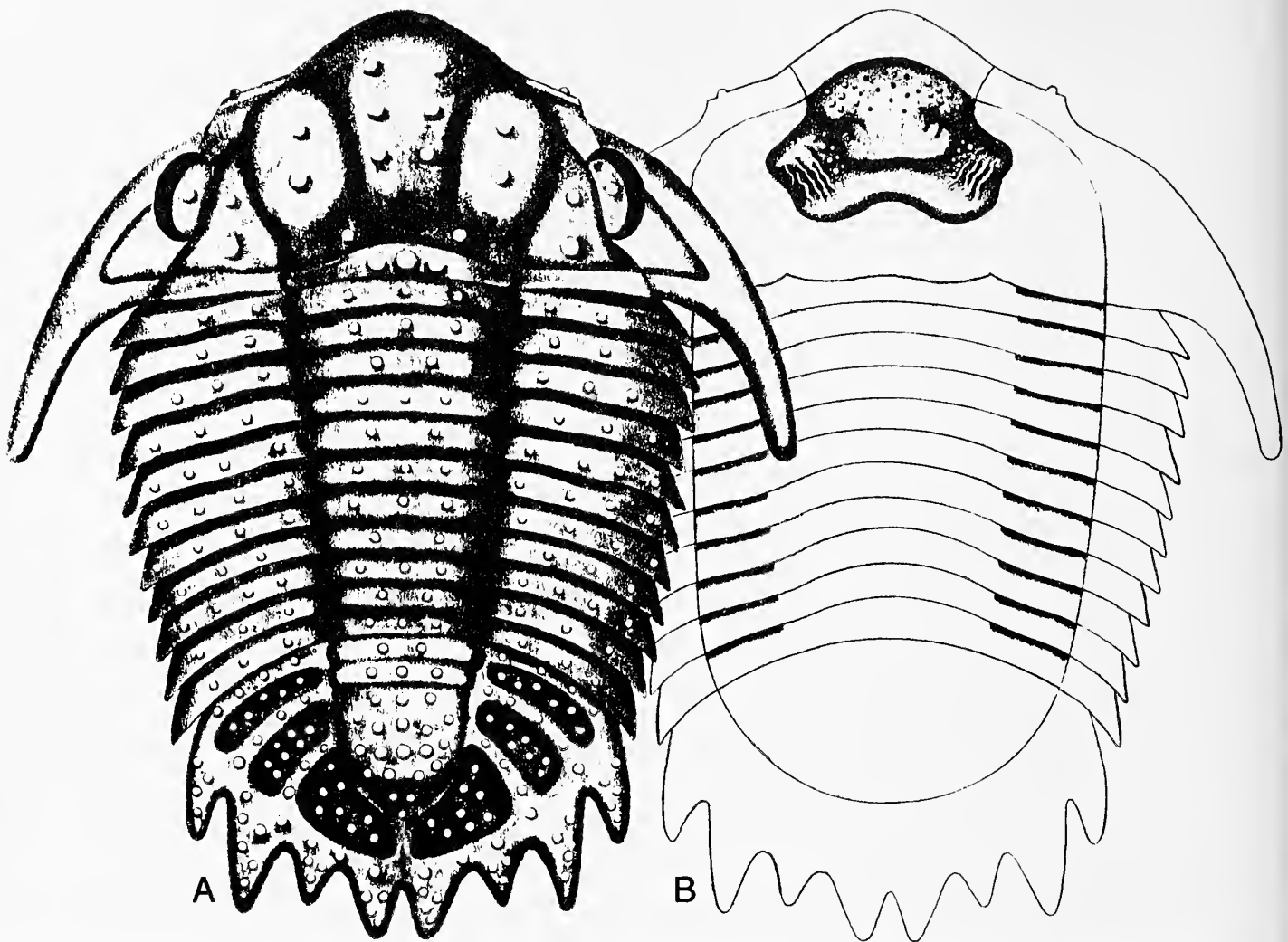


Figure 1. Reconstructions of *Hemiarges paulianus* (Clarke). Based on type material from the Prosser Formation of Minnesota and on material from the Verulam Formation of Ontario. Finer elements of prosopon omitted. A, dorsal view. B, ventral view. x3 approx.

Specimens studied for this report are deposited in the following institutions: Field Museum of Natural History, University of Chicago (UC, including Walker Museum, WM); Geological Survey of Canada, Ottawa (GSC); Royal Ontario Museum, Toronto (ROM); United States National Museum, Washington, D.C. (USNM); and Mineralogical and Geological Museum of Copenhagen (MMH).

Notation and interpretation of cranidial tubercles

Chatterton (1971, p. 34, fig. 9C; this report, Figure 2C) numbered the spine positions on the cranidium of the late protaspis of *Acanthopyge* (*Jasperia*) *bifida* (Edgell) from the Devonian, near Yass, New South Wales, Australia. Many of these positions are regularly occupied by enlarged tubercles in lichiid holaspids (Figure 2A), and Chatterton's notation is adopted herein as follows: glabellar tubercles 1-6, here prefixed "G"; G1, median occipital tubercle (if a pair of enlarged tubercles brackets the occipital tubercle, then G1 is termed "triple"); G2, on protaspis L1 (in later stages located more adaxially); G3, near base of central lobe (gradually lost in meraspis stages); G4, near midlength of central lobe; and G5 and G6, about equally spaced anteriorly. A1 is located at the rear of the fixigena, and A2 is on the fixigena

behind the eye ridge. P1 is on the palpebral lobe. In addition, a large tubercle is present on the summit of the holaspis bullar lobe between A2 and G4, with a smaller tubercle anterior and opposite to G5. These latter positions are referred to as "BL1" and "BL2" respectively. There is considerable variation in the degree of enlargement and positioning of these tubercles both in the early ontogenetic stages and the adult.

In *Hemiarges turneri turneri* and *H. turneri rasettii* (Figure 2D, E), G1, A1, and A2 are present from the early protaspis to the adult; they are enlarged on most, but not all (see Table 2) species of *Hemiarges* and many other trochurines. Tubercles on the preoccipital glabella are faint and irregular in early developmental stages. In contrast, paired tubercles are strongly developed in *Amphilichas* protaspids (Chatterton, 1980, Pl. 18, figs. 1-4, 11, 12, 15, 16, 26; Tripp and Evitt, 1981, Pl. 1, figs. 14-27), but usually absent in holaspids. Consequently, the presence of enlarged preoccipital glabellar tubercles in the adult is regarded as a synapomorphy in certain species of *Hemiarges*; their presence in the Devonian *Acanthopyge* (*Jasperia*) *bifida* appears to be an example of accelerated development, as is the case with the earlier appearance of the bullar lobes in the late protaspis of the same species.

Evitt and Whittington (1953, p. 53) discussed exoskeletal perfora-

GROUP 1 S1 INCOMPLETE, A1 & GLABELLAR TUBERCLES ENLARGED							
TAXON	CRANIDIUM					HYPO	PYG
	CON	ET	BU	CLE	AF		
<i>balanus</i>	strong	maximal	large	minimal	deep	?	clear
<i>tuberculatus</i>	strong	large	large	moderate	deep convergent	?	?
<i>troedssoni</i>	strong	large to large	large	moderate	deep convergent	?	clear
<i>paulianus</i>	strong	large	large	moderate	deep convergent	embayed	clear
<i>wesenbergensis</i>	strong	large	large	moderate	deep convergent	?	clear
<i>inghami</i>	strong	complete	moderate	narrow	moderate	transverse	strong
<i>turneri</i>	strong	complete	moderate	moderate	moderate convergent	embayed	strong
<i>E. amicus</i>	strong	complete	moderate	moderate	moderate convergent	embayed	faint
<i>E. elassouothos</i>	strong	weak	moderate	strong	moderate convergent	embayed	faint
<i>E. rasetti</i>	strong	complete	moderate	moderate	moderate convergent	embayed	absent

GROUP 2 S1 INCOMPLETE, A1 PRESENT, ENLARGED GLABELLAR TUBERCLES NOT PAIRED							
TAXON	CRANIDIUM					HYPO	PYG
	CON	ET	BU	CLE	AF		
<i>angustifrons</i>	strong	scattered	large	weak	weak subparallel	?	?
<i>zhaojianensis</i>	strong	scattered	large	moderate	deep convergent	?	absent
<i>insolitus</i>	weak	incomplete	large	strong	weak	slight bay	absent

GROUP 3 S1 INCOMPLETE, A1 PRESENT, ENLARGED TUBERCLES ABSENT							
TAXON	CRANIDIUM					HYPO	PYG
	CON	ET	BU	CLE	AF		
<i>leviculatus</i>	weak	incomplete	moderate	strong	deep subparallel	?	?

GROUP 4 S1 COMPLETE, A1 & ENLARGED GLABELLAR TUBERCLES PRESENT							
TAXON	CRANIDIUM					HYPO	PYG
	CON	ET	BU	CLE	AF		
<i>memorans</i>	strong	complete	moderate	strong	moderate subparallel	?	strong

GROUP 5 S1 COMPLETE, A1 INDISTINCT, ENLARGED GLABELLAR TUBERCLES ABSENT							
TAXON	CRANIDIUM					HYPO	PYG
	CON	ET	BU	CLE	AF		
<i>maccullochi</i>	strong	scattered	small	strong?	deep parallel	?	present
<i>diademata</i>	weak	absent	small	maximal	narrow	?	broad

NOT YET SEEN

lilaeniformis (Wigand, 1888) erratic Germany

Table 1. Distinctive characters of named species of *Hemiarges*. Abbreviations: HYPO=hypostome; PYG=pygidium; CON=convexity; ET=enlarged tubercles; BU=bullae; CLE=anterior expansion of central lobe; AF=axial furrows; PM=posterior margin; B=border; ?=not known.

tions in specimens of *Flexicalymene* and other trilobites and interpreted these as the loci of sensory hairs. Laverack and Barrientos (1985, p. 135) have suggested that some openings in the cuticle of extant crustaceans are glandular, a possibility also for trilobites. Species of *Hemiarges* display a wide range of variation in the sizes of tubercles and associated perforations. As described below, this variation includes enormously enlarged structures in *H. balanus* n. sp., by comparison with those that are barely distinguishable in *H. turneri elassouothos* n. subsp. At present, no single function can be attributed to these structures.

Systematic paleontology

Family LICHIDAE Hawle and Corda, 1847

Subfamily TROCHURINAE Phleger, 1936

Discussion.—Thomas and Holloway (1988, p. 220) have pointed out that the Subfamily Ceratarginae Tripp, 1957, is a junior synonym of the Subfamily Trochurinae.

Genus HEMIARGES Gurich, 1901

Type species.—*Lichas (Arges) wesenbergensis* Schmidt, 1885 (by subsequent designation of Reed, 1902, p. 61), Rakvere Limestone (middle Caradocian), Estonia.

Discussion.—Thomas and Holloway (1988, p. 233) limited the genus *Hemiarges* to Ordovician species with posteriorly convergent axial furrows that become faint posterior to the bullar lobes, with S1 usually incomplete, and with a broad pygidium with four pairs of marginal spines. Several species, mainly Silurian in age and formerly included in *Hemiarges*, are attributed by Thomas and Holloway (1988) to their genus *Uripes* or to *Richterarges* Phleger (1936).

HEMIARGES PAULIANUS (Clarke, 1894)

Plates 1, 2; Plate 3, figures C-I;

Plate 4, figures C-G; Figures 1, 2

Arges wesenbergensis var. *paulianus* CLARKE, 1894, p. 744, figs. 62-64 (preprint of Clarke, 1897); CLARKE, 1897, p. 744, figs. 62-64.

Hemiarges paulianus (Clarke). FOERSTE, 1920, p. 29, Pl. 2, figs. 6A-C; RAYMOND, 1921, p. 32, Pl. 9, fig. 2; KAY, 1937, Pl. 9, 2 unnumbered figs.; BOLTON AND COPELAND, in Robertson and Card, 1972, Pl. A, figs. 8, 16; LUDVIGSEN, 1978a, Pl. 5, figs. 48, 49; LUDVIGSEN, 1979, Pl. 33, Figs. A-D.

Hemiarges bartoni RAYMOND, 1925, p. 128, Pl. 8, fig. 10; BRADLEY, 1930, p. 270, Pl. 29, figs. 17-21, 24.

not *Hemiarges paulianus* (Clarke). TROEDSSON, 1928, p. 53, Pl. 15, figs. 15a-c (= *H. troedssoni* n. sp.); WILSON, 1947, p. 42, Pl. 8, figs. 7, 8; HUSSEY, 1952, p. 65, Pl. 9, fig. 14.

not *Hemiarges paulianus* (Clarke). WILSON, 1947, p. 42, Pl. 8, figs. 7, 8; HUSSEY, 1952, p. 65, Pl. 9, fig. 14.

Hemiarges aeolus SINCLAIR, 1944, p. 19, Pl. 1, figs. 5-7; SINCLAIR ET AL., 1969, Pl. 9, fig. 24.

not *Hemiarges* cf. *H. paulianus* (Clarke). DEMOTT, 1963, p. 202, Pl. 13, figs. 26-28.

Amphilichas (?) sp. BOLTON AND COPELAND, in Robertson and Card, 1972, Pl. A, fig. 7.

not *Hemiarges* aff. *H. paulianus* (Clarke). DEMOTT, 1987, p. 81, Pl. 13, figs. 26-28.

Comment on synonymy.—Part 2 of Volume 3 of the *Geology of Minnesota* was published in 1897. Winchell (1895, p. 2) reported that

SUBSPECIES ►	<u>turneri</u>	<u>amiculus</u>	<u>elassouothos</u>	<u>rasettii</u>
length (sag.) %				
max. width (tr.)	55	50	55	65
axial width %				
max. width (tr.)	45	50	40	50
axial ring #	1	1	1	2
course of axial furrow	very sigmoidal	sigmoidal	sigmoidal	straight
tubercle pair post. axis	conspicuous	small	absent	absent
2nd free point extends past 1st	yes	no	no	no
border definition	strong	weak	weak	none
FORMATION ►	Esbataottine	Crown Point	Whittaker	Edinburg
STAGE ►	Chazyan		Blackriveran	

Table 2. Summary of distinctive pygidial characters of the subspecies of *Hemiarges turneri* Chatterton and Ludvigsen.

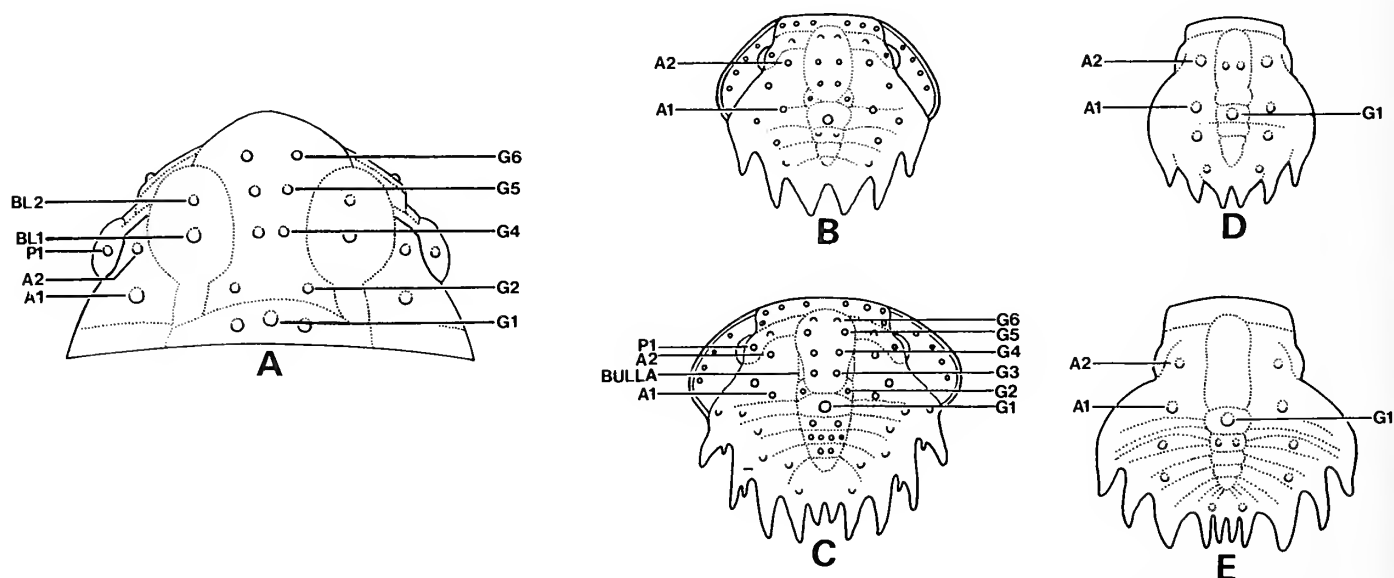


Figure 2. Cranidial tubercle notation (after Chatterton, 1971) and larval homologies. A, *Hemiarges paulianus* (Clarke). Schematic drawing of adult cranidium; x5 approx. B, C, *Jasperia bifida* (Edgell), Devonian, New South Wales, Australia. After Chatterton (1971, Fig. 9b, f). Early and late protaspids. Note appearance of the bulla in the late protaspis; x24 approx. D, E, *Hemiarges turneri rasettii* Tripp and Evitt (1981), Edinburg Formation of Virginia. Early and late protaspids; x28 approx.

preprints of Clarke's (1894) Chapter 8 on the trilobites were published on September 27, 1894. Subsequently, a note was added to Volume 3, Part 2 (Ulrich et al., 1897, p. 127) stating that the advance publication constituted a small edition of one hundred copies; no preprints were found to be available in the course of this study.

Lectotype.—Herein selected as USNM 42436a (pygidium, figured by Clarke, 1894, fig. 64), lower Prosser Limestone (late Shermanian), St. Paul, Minnesota (see Plate 1, figure E). This is the only specimen in the type series labelled as an original of Clarke's (1894) illustrations; no cranidium can be matched closely with his Figs. 62 and 63.

Topotype material.—USNM collections that include four cranidia, two hypostomes, six pygidia.

Material from other localities.—(1) One cranidium and one pygidium, apparently part of the type series, from the Decorah Shale (Blackriveran to Franklinian), 2.4 km southeast of Cannon Falls, Minnesota; (2) One cranidium, Bobcaygeon Formation (Franklinian), Kirkfield, Ontario, Columbia University Museum 25552 (illustrated by Kay, 1937, Pl. 9, one unnumbered fig.); (3) One cranidium, Bobcaygeon Formation (Franklinian), Mount Pleasant, Ontario, Columbia University Museum 25795 (illustrated by Kay, 1937, Pl. 9, one unnumbered fig.); (4) Several dorsal shields, numerous cranidia, hypostomes and pygidia, from the Bobcaygeon and Verulam Formations (Franklinian), Ontario, in collections of the Royal Ontario Museum; (5) Cranidia and pygidia, Kimmswick Limestone (Franklinian) of Missouri, Illinois, and Kentucky; (6) One cranidium (Franklinian), Chaumont, New York; (7) One cranidium, Cobourg Formation (?Edenian), Little Current, Manitoulin Island, Ontario (figured by Bolton and Copeland, 1972, Pl. A, figs. 8, 16).

Diagnosis.—A species of *Hemiarges* characterized by pygidium with abruptly constricted axis, strongly developed postaxial ridge, and well-defined posterolateral border; first and second axial rings distinct, third faint. Spines of third pygidial pleural segment almost as long as those of second.

Cranidium strongly convex, central lobe of glabella expands forward moderately; enlarged glabellar tubercles in primary positions.

Description.—Width of dorsal shields 75% of length, ovate in outline, convexity weak (sag. and tr.), axis well-defined, genal spines broad-based. Facial suture opisthoparian, rostral suture marginal. Thorax with eleven segments. Cephalon is 35% of the overall dorsal shield length (sag.), thorax 40%, pygidium 25%. Prosopon consists of a granular base with interspersed perforate tubercles. Doublure broad.

Cranidium strongly convex (sag. and tr.). Glabella 90-100% as long as wide, strongly tuberculate except in the furrows, with strongly swollen lobes and deep furrows. Occipital ring strongly arched transversely, tapers to a point abaxially and slopes anteriorly. Occipital furrow deep and broad abaxially, shallowing mesially. Central lobe strongly swollen and rises higher than bullar lobes, moderately expanded anteriorly where it extends halfway across bullar lobe, narrows strongly and uniformly posteriorly. Longitudinal furrows deep and broad, convergent posteriorly, dies out at back of bullar lobe, but extended by a shallow granular depression to occipital furrow. Bullar lobe 45-50% length (sag.) of cranidium in normal view, slightly wider than central lobe opposite eye, strongly convex. L1 short, 10% length of cranidium adaxially, partially fused with bulla, faintly separated from central lobe by extension of longitudinal furrow and from fixigena by extension of axial furrow, rarely depressed. L1a subelliptical, steeply inclined, confluent with L1b and strongly demarcated from occipital ring. Preglabellar furrow well-defined, undercuts central lobe. Anterior border moderately wide, expands slightly opposite axial furrow. Axial fur-

row strong anteriorly, shallows backward, curves gently inward alongside bullar lobe, then continues almost straight back to occipital furrow as a granular extension. Eye ridge narrow, strong, extends backward and outward from anterolateral angle of glabella to palpebral lobe. Palpebral lobe crescentic, 20% length of cranidium, slopes inward, posterior extremity placed opposite S1. Palpebral furrow shallow. Fixigena convex, postocular area subtriangular, slopes steeply outward and backward, almost twice as long (exsag.) abaxially as adaxially. Posterior border short, set low compared with occipital ring and fixigena. Posterior border furrow deep, widens abaxially. Anterior branch of facial suture runs forward and abaxially alongside eye ridge, cuts anterior margin at a steep angle; posterior branch curves outward and backward, crosses posterior border near midwidth.

Eye lobe large, pedunculate but short, lens surface weakly convex, occupies upper two-thirds of lobe. Socle gently convex, constricted at base. Librigena falcate, lateral margin sigmoidal in outline. Field small, lateral and posterior borders wide and strongly swollen, merges to form a backwardly curving stubby genal spine that extends to the second thoracic segment. Field and socle coarsely granular; border with terrace ridges anteriorly.

Prosopon of cephalon ranges from coarse tuberculation to granulation, large granules and tubercles with single or multiple perforations at summit. Largest paired tubercles appreciably but variably larger than others, usually in the following positions: G1 (triple), G4, G5, BL1, A1. Smaller paired tubercles are G2, G6, BL2, A2, P1. Some cranidia (e.g., Plate 1, figures A, B) are more coarsely tuberculate overall than others of the same size. Lateral tubercle on anterior border slightly enlarged. Borders of librigena coarsely tuberculate.

Hypostome 55% as long (sag.) as wide. Central body broadly rounded in front, 66% length (sag.) of hypostome, and weakly convex. Posterior lobe narrow (tr.), convex; small, swollen oval macula set obliquely at anterior inner corner. Middle furrow transverse, short. Lateral and posterior furrows strong, broader on internal than on external surface. Lateral margin curves strongly outward and backward at front, forms swollen anterior wing, convex back posteriorly. Posterior margin with broad median embayment 35% width and 20% length (sag.) of border. Posterior border separated from swelling on posterior wing by broad shallow depression. Doublure of posterior border reaches almost as far as posterior border furrow, gently convex except for a ventrally convex median boss that is half the length of the border. Middle body granular anterolaterally, shallowly pitted mesially. Posterolateral border granular laterally with interspersed terrace ridges convergent backward. Prosopon faint mesially.

Thorax composed of eleven segments. Axial rings simple, narrowing little abaxially. Articulating half-rings short, articulating furrows deep. Pleurae directed slightly backward. Posterior band strongly swollen and ends in a short outwardly directed free point; anterior band depressed. Pleural furrow indistinct. Axial rings and posterior bands bear a row of strong tubercles.

Pygidium 60-65% as long (sag.) as wide. Axis 40% maximum width of pygidium, strongly arched transversely, narrows strongly at 40% of pygidial length from front; postaxial ridge narrow, strongly developed, merges with border. First and second rings complete, third faint. Axial furrow deep anteriorly, shallows backward, well-defined. Pleural lobe moderately convex. First pleura narrow (tr.), extended into free point. Anterior band less swollen than posterior band, marked off by pleural furrow that dies out at base of free point. Second pleura similarly constructed, but larger and wider (tr.) and expands more strongly abaxially. Posterolateral border swollen and marked off chiefly from anterior band

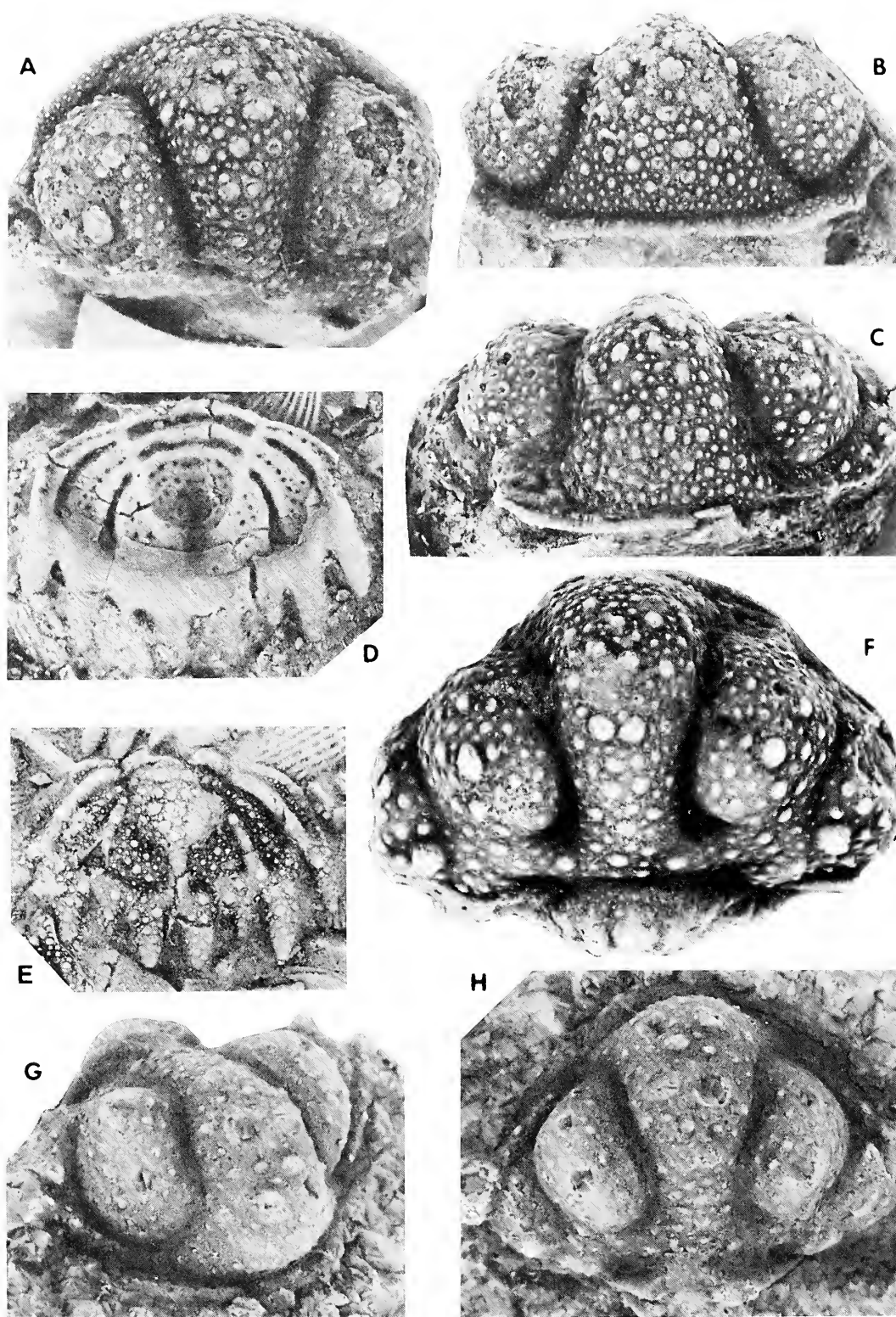


Plate 1. *Hemiarges paulianus* (Clarke). *A, B*, Dorsal and anterior views of incomplete cranium, x8. USNM 42437. Prosser Limestone, St. Paul, Minnesota. *C, F*, Anterior and dorsal views of cranium, x5. GSC 13276. Holotype of *Hemiarges aeolus* Sinclair (1944, Fig. 1, figs. 5-7; Ludvigsen, 1978, Pl. 5, fig. 48). Verulam Formation, Lakefield Quarry, Lakefield, Ontario. *D*, Ventral view of pygidium, x8. USNM 7836e. Prosser Limestone, St Paul, Minnesota. *E*, Dorsal view of lectotype pygidium, x8. USNM 42436a. Figured by Clarke (1894, Pl. 64) and Ludvigsen (1978, Pl.5, fig. 49). Prosser Limestone, St. Paul, Minnesota. *G, H*, Oblique lateral and dorsal views of cranium, x8. MCZ 1755. Holotype of *Hemiarges bartoni* Raymond (1925, Pl. 10, fig. 8). Kimmswick Limestone, Mincke, Missouri.

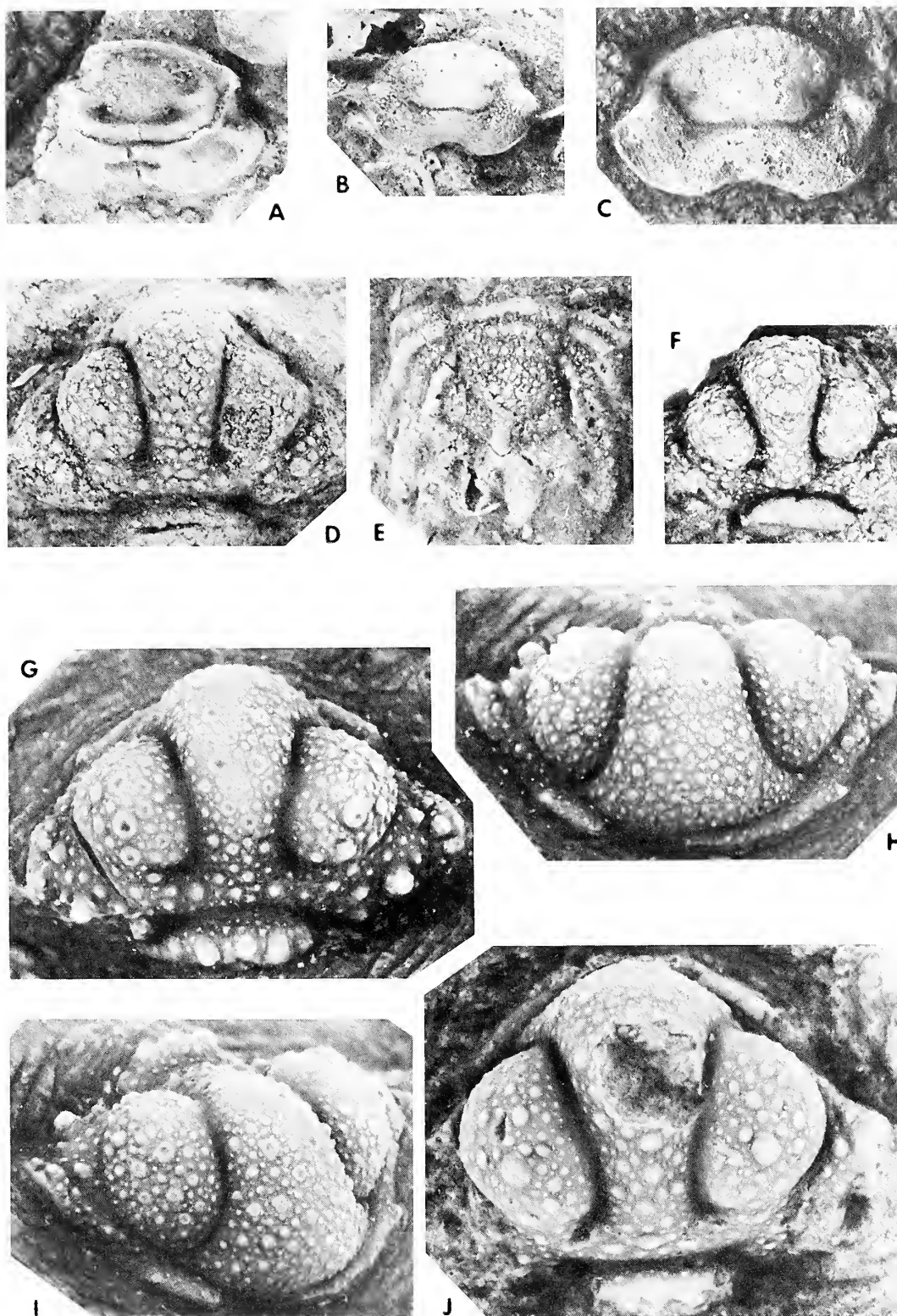


Plate 2. *Hemiargus paulianus* (Clarke). A, Dorsal view of hypostome, x8. USNM 42436e. Prosser Limestone, St. Anthony Hill, St. Paul, Minnesota. B, Ventral view of hypostome, x8. USNM 42436d. Same locality as A. C, Ventral view of hypostome, x5.8. ROM 35356. Verulam Formation, right bank of Moira River, Belleville, Ontario. D, Dorsal view of cranidium, x8. USNM 78365c. Prosser Limestone, St. Paul, Minnesota. E, Dorsal view of pygidium, x8. USNM 8365a. Prosser Limestone, St. Paul, Minnesota. F, Dorsal view of cranidium, x8. ROM 35394. Verulam Formation, right bank of Moira River, Belleville, Ontario. G, H, I, Dorsal, anterior, and oblique lateral views of cranidium, x8. ROM 35395. Verulam Formation, Lakefield Quarry, Lakefield, Ontario. J, Dorsal view of cranidium, x8. ROM 35355. Verulam Formation, right bank of Moira River, Belleville, Ontario.

by broad border furrow. Third pleura unfurrowed, area inside border gently swollen and circumscribed by pleural and border furrows. Posterolateral border broad, swollen, and well-defined; border furrow broad and shallow. Posterior free points of third pleurae almost as large as those of second, separated by a narrow U-shaped notch; anterior pair much shorter but broad-based. Doublure 30% length (sag.) of pygidium, convex posteriorly, concave anteriorly; anterior margin simple. Terrace ridges fine, closely spaced. Dorsal surface strongly granular; single rows of tubercles on axial rings, a small pair on terminus.

Distribution.—The common *Hemiarges* species from the Verulam Formation (Shermanian) of Ontario is *H. paulianus*, and this description is based partly on Verulam material. A cranidium from the Verulam Formation at Lakefield Quarry was designated as the holotype of *H. aeolus* by Sinclair (1944, p. 19, Pl. 1, figs. 5-7; Ludvigsen, 1978, Pl. 5, fig. 48; see Plate 1, figures C, F). This species is considered a synonym of *H. paulianus*. The species occurs less commonly in the Bobcaygeon and Cobourg Formations of Ontario.

Cranidia and pygidia from the Kimmiswick Limestone (Franklinian) of Missouri also belong to *Hemiarges paulianus* and differ only in the less-dense prosopon. The arrangement of large tubercles is closely similar, although the occipital tubercles are less conspicuous. A cranidium from the Kimmiswick Limestone at Mincke, Missouri, is the holotype (by monotypy) of *Hemiarges bartoni* Raymond (1925, p. 128, Pl. 8, fig. 10; see Plate 1, figures G, H of this report and Bradley, 1930, Pl. 29, figs. 17-21, non fig. 24 (= *H. leviculus*)). *Hemiarges bartoni* is herein considered to be a junior subjective synonym of *H. paulianus*.

A cranidium in the USNM (see Plate 3, figures C-E), from the Franklinian of New York, agrees in all diagnostic features with *Hemiarges paulianus*. Although the main tubercles are somewhat larger, the cranidium is referable without hesitation to this species.

The single cranidium identified as *Hemiarges* aff. *paulianus* by DeMott (1963, 1987, p. 81, Pl. 13, figs. 26-28) from the Mifflin Formation of the Platteville Group (Blackriveran) at Dixon North, Illinois, resembles *H. paulianus* in glabellar construction. However, it differs in the finer tuberculation and lack of large tubercles and may be only distantly related.

Comparison with other species.—As Clarke (1894) correctly observed, *Hemiarges paulianus* bears a close resemblance to the type species *H. wesenbergensis* (Schmidt, 1885, p. 44, Pl. 6, fig. 1; see also Öpik, 1937, p. 63, Pl. 22, fig. 7; Thomas and Holloway, 1988, figs. 214, 218, 219) from the Rakvere Limestone (Caradocian) of Estonia. *Hemiarges paulianus* differs from *H. wesenbergensis* in the following features: (1) the longitudinal convexity of the cranidium is much stronger and overhangs the anterior border; (2) the tuberculation is more uniform on the front of the central lobe; (3) the anterior border widens more strongly laterally; (4) the bullar lobes are wider; (5) the palpebral lobes are smaller; (6) the pygidium is shorter; (7) the third and fourth ring furrows are weaker and absent, respectively; (8) the first and second anterior pleural bands are much narrower; and (9) the marginal free points on the pygidium, particularly the anterior pair on the third segment, are shorter.

Other related species with comparable arrangements of large tubercles are known. These include *Hemiarges paulianus* (Clarke) of Troedsson (1928, p. 53, Pl. 15, figs. 15a-c) from the Cape Calhoun Beds (Edenian or Maysvillian) at Cape Calhoun, northern Greenland (Plate 4, figure B). This species differs from *H. paulianus* in that G5 is much larger than G4 and is granular. The central lobe is more widely expanded anteriorly; it decreases in width strongly at first, then more steadily to become narrow posteriorly. The name *Hemiarges troedssoni*

n. sp. is proposed for this species.

Hemiarges inghami Tripp (1979, p. 354, Pl. 40, figs. 1-17; 1967, p. 81, Pl. 6, fig. 26) from the Stinchar Limestone (Llanvirnian–Llandeilian) of the Girvan district, Scotland, has an array of enlarged tubercles identical to that of *H. paulianus*. The former differs in that it has the following features: (1) narrower glabellar lobes; (2) shorter, less-swollen bullar lobes; (3) paired occipital spines; (4) more slender genal spine; (5) unembayed posterior margin of the hypostome; and (6) pygidium with paired tubercles and very small free points on the posterior margin.

Most of the distinctive features of *Hemiarges wesenbergensis* and *H. paulianus* are shared with *H. turneri* Chatterton and Ludvigsen (1976, p. 85, Pl. 19, figs. 1-41; Chatterton, 1980, p. 56, Pl. 17, figs. 1-23) and its subspecies. The main differences are that the tuberculation is more subdued, the central lobe is broader, and the bullar lobes are narrower in *H. turneri*.

The poorly preserved holotype cranidium of *Hemiarges tuberculatus* (Weller, 1903) from the Franklinian of New Jersey (Plate 4, figure A), demonstrates close systematic relationships to *H. paulianus*. Similarities include its swollen glabellar lobes; undepressed L1; enlarged and granular G5; and small but distinct BL1, BL2, and A1. The G4 is represented by a single large scar on the right side. *Hemiarges* cf. *tuberculatus* of Westrop and Ludvigsen (1983, p. 26, Pl. 9, figs. 3, 4) from the Selkirk Member of the Red River Formation (Edenian?) in southern Manitoba is closely similar. It is interesting that it also has a single G4, in this case mesially placed. *Hemiarges tuberculatus* and *H. cf. tuberculatus* also differ from *H. paulianus* in possessing a more prominent central lobe that decreases in width steadily backward to become narrow posteriorly. In this feature, they both resemble *H. troedssoni* n. sp.

Several *Hemiarges* species differ from *H. paulianus* in having paired and enlarged primary tubercles (A1, A2) only on the fixed cheek and in the weaker convexity of the cranidium and glabellar lobes. These include *Hemiarges leviculus* Bradley (1930, p. 271, Pl. 29, figs. 22, 24) from the Kimmiswick Limestone (Shermanian) of Missouri and Illinois (see Plate 3, figure B); *H. insolitus* Tripp (1967, p. 80, Pl. 6, figs. 20-25) from the Stinchar Limestone (Llanvirnian–Llandeilian) of Auchensoul; *H. angustifrons* Tripp (1954, p. 662, Pl. 1, figs. 20-23) from the Kiln Mudstones (upper Caradocian) at Craighead Quarry; and an unnamed species from the Girvan district, Scotland. In addition, *H. zhaobishanensis* Zhou, Lee, and Qu (1982, p. 292, Pl. 72, figs. 5-6) from the Miaopo Formation of the Yaomoshan Group (Caradocian) of Yumen County, Gansu Province, northwestern China, and material in the USNM from Kentucky, Indiana, Ohio, Tennessee, and Wisconsin also share these features. The cranidium attributed to *H. paulianus* by Hussey (1952, p. 65, Pl. 9, fig. 14) from the Chandler Falls Member (Franklinian) of the Escanaba River area, Michigan, lacks large glabellar tubercles, and falls into this group.

Hemiarges memorans Öpik (1937, p. 64, Pl. 22, fig. 1, Pl. 23, figs. 1-2) from the Porkuni Formation (Himantian) of Estonia is set apart by the complete S1 and, consequently, circumscribed bullae. In *H. turneri* meraspid, the bullar lobes remain circumscribed, and this is taken to be the primitive condition, with an incomplete S1 being a derived state. Other differences between *H. paulianus* and *H. memorans* are the broad central lobe, short and gently swollen bullae, shallow cranial furrows, and long pygidial free points in the latter. *Hemiarges memorans* has a complete set of enlarged tubercles that are clearly illustrated by Öpik (1937, Fig. 18), an example of recurrence of this feature in a distantly related lineage.

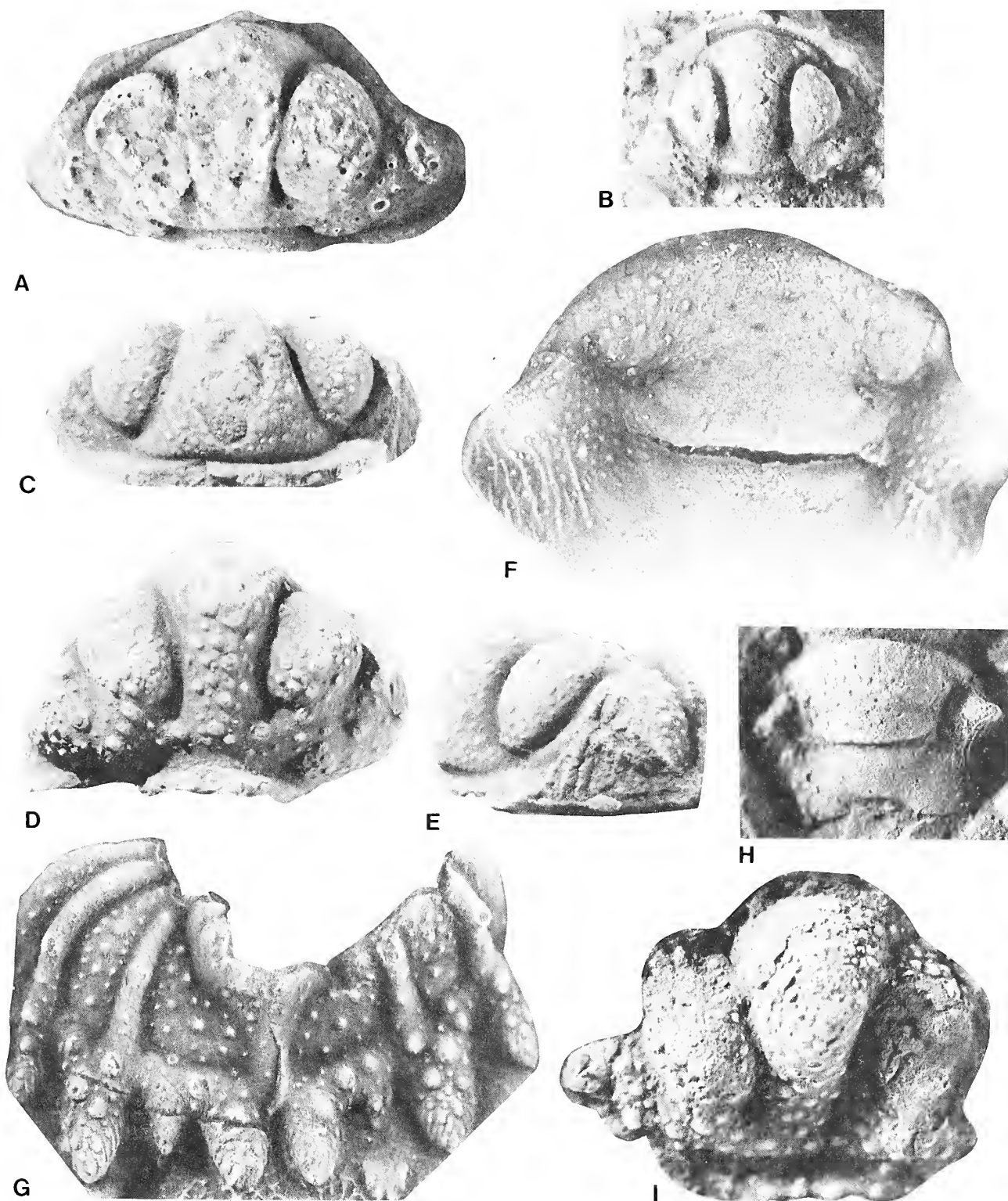


Plate 3. *Hemiarges* species. A, *H. warburgae* Troedsson. Dorsal view of holotype cranium, x5. MMH255. Cape Calhoun Formation, Cape Calhoun, northern Greenland. B, *H. leviculus* Bradley. Dorsal view of holotype cranium, x7. WM 28042. Figured by Bradley (1930, Pl. 22, fig. 29). Kimmswick Limestone, near Batchtown, Illinois. C, D, E, *H. paulianus* (Clarke). Cranium, frontal, dorsal and left lateral views, x5. USNM 78362. Franklinian, Chaumont, New York. F, *H. paulianus* (Clarke). Hypostome, x16.3. ROM 45387. Verulam Formation, Mara Quarry, Gamebridge, Ontario. G, *H. paulianus* (Clarke). Pygidium, x10. ROM 45389. Verulam Formation, Mara Quarry, Gamebridge, Ontario. H, *H. paulianus* (Clarke). Hypostome, x7.0. ROM 46080. Bobcaygeon Formation, Brechin, Ontario. I, *H. paulianus* (Clarke). Cranium, x6.5. ROM 46081. Bobcaygeon Formation, Brechin, Ontario.

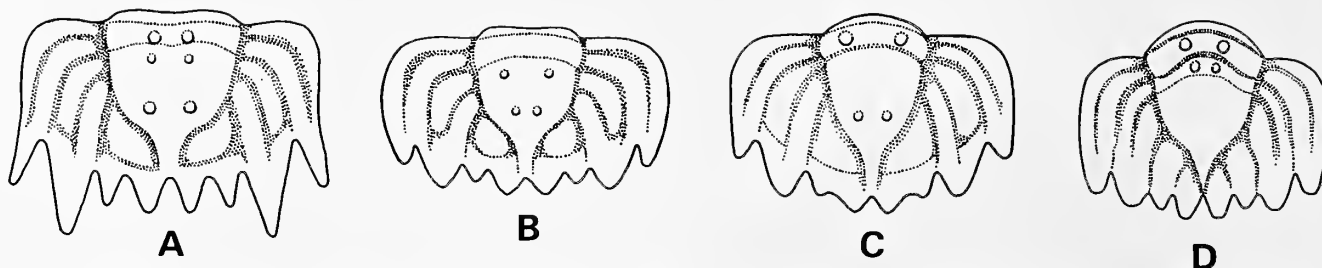


Figure 3. Restorations of pygidia of the subspecies of *Hemiarges turneri* Chatterton and Ludvigsen, 1976. A, *Hemiarges turneri turneri* Chatterton and Ludvigsen (see Plate 5, figure T), lower part of Esbataottine Formation, District of Mackenzie, Canada, x8.5. B, *Hemiarges turneri amicus* n. subsp. from the Chazy Group (after Shaw, 1968, Pl. 3, fig. 16), x16. C, *Hemiarges turneri elassouothos* n. subsp. (see Plate 5, figure S), upper part of Esbataottine Formation, District of Mackenzie, Canada, x11.5. D, *Hemiarges turneri rasettii* Tripp and Evitt (1981, Pl. 2, fig. 21), Edinburg Formation of Virginia, x9.

Other species of *Hemiarges* with complete S1 include *H. maccullochi* (Reed, 1914, p. 28, Pl. 4, figs. 9, 10; Tripp, 1959, Fig. 393, 8a; Morris and Tripp, 1986, p. 174, Pl. 4, fig. 6), from the Starfish Bed of the South Threave Formation (Rawtheyan) at South Threave, Girvan District, Scotland, and *H. diadayma* n. sp. from the lower Whittaker Formation (Edenian) in the District of Mackenzie, Canada. Both of these species lack enlarged tubercles on the cranidium.

Hemiarges warburgae Troedsson (1928, p. 51, Pl. 16, figs. 3a, b) from the Cape Calhoun Formation (Edenian or Maysvillian) at Cape Calhoun, northern Greenland, lacks enlarged tubercles. It has a broad, weakly swollen central lobe that is widely expanded anteriorly, narrows abruptly backward initially, and then more gently. Additional features include bullar lobes with strong independent convexity, strongly developed but apparently incomplete S1, and broad fixigenae. It is unlike other *Hemiarges* species in many respects. The pygidium illustrated as *Amphilichas obtusicaudatus* by Troedsson (1928, p. 50, Pl. 16, fig. 2) probably belongs to this species; it lacks the characteristic border and four pairs of marginal spines of *Hemiarges*, but the postaxial ridge is unlike that of *Amphilichas*. If this association proves to be correct, the species should certainly be referred to *Uripes*, as Thomas and Holloway (1988, p. 238) have done.

Figures 4 and 5 summarize the inferred phylogenetic and known stratigraphic distributions, respectively, of species of *Hemiarges* with enlarged glabellar tubercles.

HEMIARGES TROEDSSONI n. sp.

Plate 4, figure B

Hemiarges paulianus (Clarke, 1894). TROEDSSON, 1928, p. 53, Pl. 15, figs. a-c.

Diagnosis.—A species of *Hemiarges* with granular G5 much larger than G4 and a central lobe that is broadly expanded anteriorly, strongly contracted initially, then decreases in width more steadily to become narrow posteriorly; granulation dense and even.

Holotype.—University of Copenhagen MMH 426271 (cranidium, figured by Troedsson, 1928, Pl. 15, figs. a-c) from the Cape Calhoun Formation (Edenian or Maysvillian), Cape Calhoun, northern Greenland; see Plate 4, figure B.

Discussion.—This species differs from *Hemiarges paulianus* in possessing a granular G5 that is larger than G4 and in the shape of the central lobe. In addition, it is characterized by such minor features as much narrower and less-swollen bullar lobes, weaker glabellar furrows, and more complete fusion of the bullar lobe and L1. For comparison with other named species of *Hemiarges*, see Table 2.

Etymology.—After Dr. Gustaf Troedsson, in honor of his fine work on the Lower Paleozoic faunas of northern Greenland.

HEMIARGES TURNERI TURNERI Chatterton and Ludvigsen, 1976

Plate 5, figures B, C, E-G, I, L, M, P, R, T; Figure 3A

Hemiarges turneri CHATTERTON AND LUDVIGSEN, 1976, p. 85, Pl. 19, figs. 1-41; CHATTERTON, 1980, p. 56, Pl. 17, figs. 1-23.

Holotype.—GSC 43450 (cranidium, figured by Chatterton and Ludvigsen, 1976, Pl. 19, figs. 6, 12, 13), locality A 110, lower Esbataottine Formation (Whiterockian), Mackenzie Mountains, District of Mackenzie, Canada.

Discussion.—Chatterton and Ludvigsen (1976) considered both the material from the Chazy Group of New York (Shaw, 1968, p. 89, Pl. 3, figs. 8, 10, 11, 14-22, 24) and from the Edinburg Formation of Virginia (Hu, 1974, p. 357, Pl. 49, figs. 1-14, 19-30) to belong to *Hemiarges turneri*. The latter was subsequently described as *H. turneri rasettii* by Tripp and Evitt (1981), and the former is described below as *H. turneri amicus* n. subsp. In addition, a third subspecies, *H. turneri elassouothos* n. subsp., is herein described from the uppermost Esbataottine Formation (Blackriveran). The type subspecies differs from the others by its longer and narrower pygidial free points and by the projection of the second beyond the third (Figure 3). The slight differences in cranidial convexity and enlargement of tubercles is illustrated by side-by-side comparison on Plate 5.

HEMIARGES TURNERI AMICULUS n. subsp.

Figure 3B

Amphilichas minganensis SHAW, 1968, p. 89, Pl. 3, figs. 8, 10, 11, 14-22 (non Pl. 3, figs. 2-7, 9, 12, 12, 23, 25; Pl. 4, fig. 1; =*Amphilichas minganensis*).

Diagnosis.—A subspecies of *Hemiarges turneri* characterized by pygidium with short, stubby free points; tips of those on second pleura extend no farther back than posteriormost pair. Pygidial border broad and moderately well-defined, axis short, course of axial furrow moderately sigmoidal.

Holotype.—NYSM 12228 (silicified pygidium, figured by Shaw, 1968, Pl. 3, figs. 16, 19), locality PB81, Crown Point Formation, 24.3 m above base of section measured from near top of Day Point Formation at east end of Pebble Beach, center of south shore at Valcour Island, New York.

Description.—Cranidia as in *H. turneri turneri* Chatterton and Ludvigsen (1976, p. 85, Pl. 19, figs. 1-41) except that convexity is weaker and glabellar tubercles are slightly less well-developed. Hypostome closely similar, with the scattered anterior tubercles and coarse pitting of middle body.

The distinction of *Hemiarges turneri amicus* n. subsp. from *H. turneri turneri* lies in the pygidium, which differs as follows: (1) the free points are short and stubby, with the second extending backward

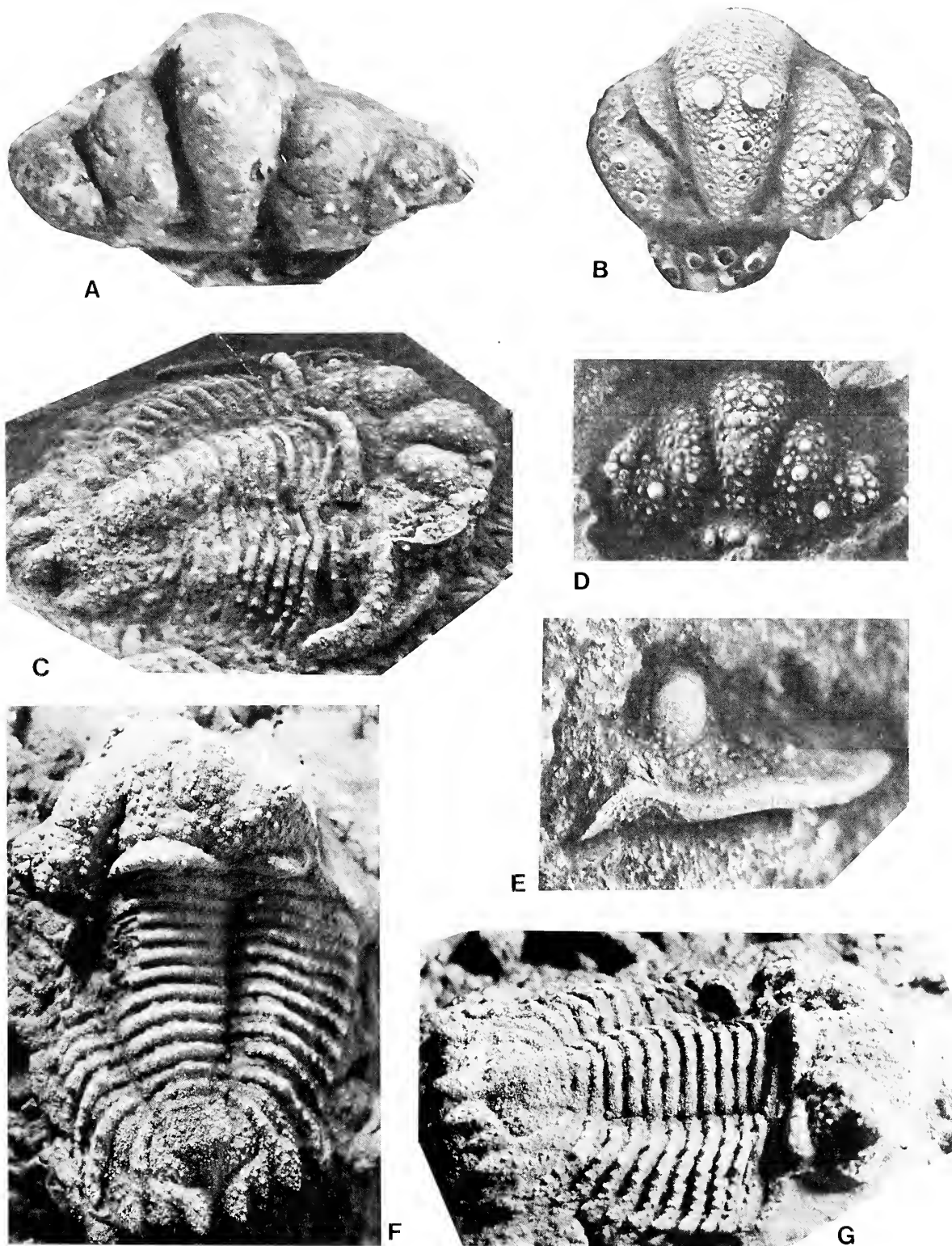


Plate 4. *Hemiarges* species. *A*, *H. tuberculatus* Weller. Dorsal view of holotype cranium, x7. UC 10265. Franklinian, near Iliff's Pond, New Jersey. *B*, *H. troedssoni* n. sp. Dorsal view of holotype cranium, x5. MMH 426271. Cape Calhoun Formation, Cape Calhoun, northern Greenland. *C-G*, *H. paulianus* (Clarke). Verulam Formation, Ontario. *C*, Dorsal shield, oblique right lateral view, x6.5. Mara Quarry, Gamebridge, Brewster Collection. *D*, Dorsal view of small cranium, x13.0. ROM 45394. Mara Quarry, Gamebridge. *E*, Lateral view of left librigena, x15. ROM 45392. Lakefield Quarry, Lakefield. *F*, *G*, Dorsal shield; dorsal and oblique right lateral views, x5. Tatematsu Collection, Mara Quarry, Gamebridge.

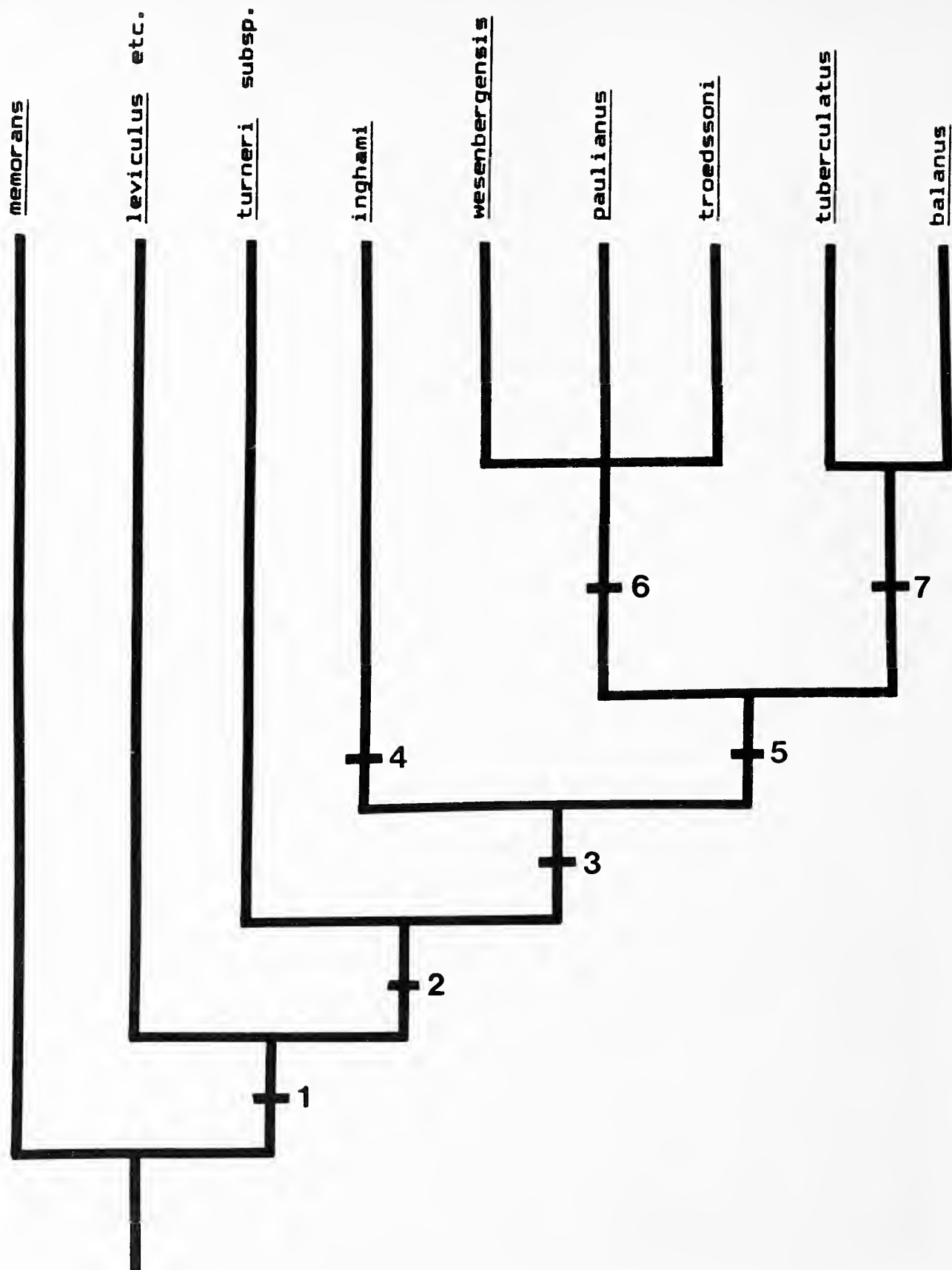


Figure 4. Cladogram depicting inferred relationships among named species of *Hemiarges* with enlarged glabellar tubercles. Characters indicated by short horizontal black bars. 1, S1 incomplete. 2, Full array of glabellar tubercles. 3, Tubercle array conspicuously enlarged. 4, Paired occipital spines. 5, G5 and/or G4 large. 6, Frontal lobe broad. 7, G4 single. Cladogram illustrates the apparently convergent development of relatively enlarged glabellar tubercles in two distinct groups within the *Hemiarges* lineage: those characterized by *H. memorans* with complete S1, and by *H. paulianus* with S2 incomplete. It also suggests the coordinate development of such features as a narrow frontal lobe and enormously enlarged tubercles (with some loss of pairing), as in the *H. balanus*–*tuberculatus* group.

	NORTH AMERICA	GREENLAND	SCOTLAND	ESTONIA
Hirnantian				<u>memorans</u>
Edenian?	<u>balanus</u>	<u>troedssoni</u>		<u>wesenbergensis</u>
Franklinian	<u>paulianus</u> <u>tuberculatus</u> t. <u>elassouothos</u>			
Blackriveran	t. <u>rasettii</u>			
	t. <u>aff. rasettii</u>			
Whiterockian	t. <u>turneri</u> t. <u>amiculus</u>		<u>inghami</u>	

Figure 5. Geographic and stratigraphic distribution of named species of *Hemiarges* with enlarged glabellar tubercles.

no farther than the most posterior, and a much shorter anterior free point on the third segment; (2) the posterolateral border is broader and more weakly defined; and (3) the axis is shorter.

Discussion.—Although the New York material is limited, the holotype pygidium is clearly distinct from the abundant Esbataottine material. *Hemiarges turneri amicus* n. subsp. resembles *H. turneri rasettii* in the short free points, but differs in the gently tapering axis and more strongly defined border. It differs from *H. turneri elassouothos* n. subsp. in the short axis and much shorter free points.

Etymology.—*amicus* n. sp., abounding in friends (L.).

HEMIARGES TURNERI RASETTII Tripp and Evitt, 1981
Figure 3D

Amphilichas cf. *prominulus* (Raymond). HU, 1974, p. 357, Pl. 49, figs. 1, 5-14, 18-29.

Hemiarges turneri rasettii TRIPP AND EVITT, 1981, p. 666, Pl. 1, figs. 1-13, Pl. 2, figs. 17-21.

Holotype.—BM It. 12508 (pygidium, illustrated by Tripp and Evitt, 1981, Pl. 2, fig. 21), locality 3 of Whittington and Evitt (1953), Botetourt Member, Edinburg Formation, Virginia.

Other Material.—Specimens, including protaspids and meraspids, are very common at localities 3 and 4 of the Edinburg Formation (Blackriveran). Cranidia and pygidia at localities 1 and 1a from the lower and upper parts of the Lincolnshire Limestone may belong to this subspecies.

Discussion.—This subspecies is characterized by a degree of cranial convexity and tubercle enlargement that falls between that shown by *Hemiarges turneri turneri* and *H. turneri amicus* n. subsp., on one hand, and *H. turneri elassouothos* n. subsp., on the other. It is not possible to distinguish between the latter three subspecies on cranial characters alone. In pygidial features, particularly in the gradual narrowing of the axis, *H. turneri rasettii* shows the most extreme differentiation. Incomplete pygidia from the Lincolnshire Formation (Tripp and Evitt,

1981, p. 670, Pl. 2, figs. 13-16), formerly attributed to an unnamed subspecies, resemble those of *H. turneri rasettii* in the gradually tapering axis, but differ in having only one axial ring and larger paired tubercles at the back of the axis. As suggested by Tripp and Evitt (1981), the form from the Lincolnshire Formation is clearly ancestral to *H. turneri rasettii*; we refer to this material under open nomenclature as *H. turneri* subsp. indet. aff. *H. turneri rasettii*.

HEMIARGES TURNERI ELASSOUOTHOS n. subsp.
Plate 5, figures A, D, H, J, K, N, O, Q, S, U; Figure 3C

Diagnosis.—A subspecies of *Hemiarges turneri* with glabellar tubercles scarcely enlarged over background granulation. Genal spine short. Axis of pygidium with two rings, axis narrows gradually backward; free point of second pleura extends backward no farther than most posterior pair, border weakly defined.

Holotype.—ROM 46086 (pygidium, Plate 5, figures O, S, U), uppermost part of Esbataottine Formation (Franklinian), locality P2038, Sunblood Range, Mackenzie Mountains, District of Mackenzie, Canada.

Topotype material.—Abundant cranidia, librigenae, hypostomes, and pygidia from locality P2038.

Description.—Cranidia as in *H. turneri turneri* Chatterton and Ludvigsen (1976, p. 85, Pl. 19, figs. 1-41), except that glabellar tubercles are much less-strongly developed, longitudinal convexity is weaker, and the frontal lobe is more widely expanded. Librigena with shorter genal spine. Hypostome similar to that of *H. turneri turneri*, with scattered anterior tubercles and strongly pitted middle body.

Discussion.—The main distinction between *H. turneri turneri* and *H. turneri elassouothos* n. subsp. lies in the pygidium of the latter, which differs as follows: (1) free points are broader, second pleura extends backward no farther than the posteriormost, and anterior free point on third segment is much shorter; (2) posterolateral border is broader and more weakly defined; (3) axis narrows more gradually posteriorly; and

(4) paired tubercles on the first ring and on terminus are farther apart and much smaller. The cranium of *H. turneri elassouothos* n. subsp. differs from that of other subspecies in the slight enlargement of the glabellar tubercles and weaker convexity. The distinctive features of the pygidium are summarized in Table 2 and Figure 3.

Etymology.—*elassouothos* n. subsp., "dwindle" (Gk.), in reference to the relatively small degree of enlargement of glabellar tubercles.

HEMIARGES BALANUS n. sp.

Plate 6, figures A-J

Diagnosis.—A species of *Hemiarges* with greatly enlarged cranial tubercles, single G4, and perforations up to half the diameter of tubercles. Central lobe widens slightly frontally and is strongly convex. Pygidium with long, slender free points, second pair extend backward much farther than posteriormost; border narrow, clearly defined; axis narrows gradually backward.

Holotype.—ROM 46087 (cranium, Plate 6, figures A, B, D), lower part of the Whittaker Formation (Edenian), locality H1920, Whittaker Range, Mackenzie Mountains, District of Mackenzie, Canada.

Topotype material.—Seven cranidia, one pygidium.

Description.—Cranidium resembles that of *H. paulianus* in the strong longitudinal convexity, strong independent swelling of the glabellar lobes, deep furrows, narrow anterior border that widens abaxially, and small L1. It differs from the cranium of *H. paulianus* in several ways: (1) it is more elongate; (2) the frontal lobe widens only slightly anteriorly; and (3) the cranial tubercles are greatly enlarged, granular overall, and coarsely perforate. In addition, the paired tubercles on the occipital ring are larger and placed farther back than G1. In the array of greatly enlarged tubercles, G5 is largest and occupies 25% of the maximum width of the central lobe; G4 is comparatively small, single, and off-center; BL1 is larger than A1.

Pygidium is much like that of *H. turneri turneri*, but is narrower. Free points are longer except for the anterior points of the third pleurae, the axis narrows more gradually backward, and the pair of small tubercles at the back of the axis is replaced by a single large tubercle. The larger elements in the prosopon are perforate.

Discussion.—*Hemiarges balanus* n. sp. is immediately distinguishable from all other known species by the enormous size of the cranial tubercles. The closest resemblance is to *H. tuberculatus* in the narrow, prominent central lobe, single G4 that is sometimes off-center, and strong convexity. The cranium resembles that of *H. paulianus* much more closely than *H. turneri* in the convexity of the lobes, strength of the furrows, and greater enlargement of the cranial tubercles, but differs from both in the narrow frontal lobe. The reverse is the case with the pygidium, which resembles *H. turneri turneri* and differs from *H. paulianus* in the long slender free points. These features demonstrate the dissociation between cranial and pygidial morphology often seen in species of *Hemiarges*. Although the perforations in the tubercles are abraded in some specimens, this is not the case in others, and they must have been about half the diameter of the tubercles—up to 0.2 mm in diameter.

Etymology.—*balanus* n. sp., from *Balanus* (L.), the genus of the common acorn barnacle, in allusion to the heavily encrusted appearance of specimens.

HEMIARGES DIADAYMA n. sp.

Plate 6, figures K-S

Hemiarges sp. LUDVIGSEN, 1978b, Pl. 2, fig. 16.

Diagnosis.—A species of *Hemiarges* without enlarged tubercles on

the cranium. Bullar lobes small and circumscribed. Cranial convexity weak. Anterior border broad. Pygidium with free point of second pleura extending backward no farther than posteriormost pair, border weakly defined, and axis narrowing gradually backward.

Holotype.—ROM 46091 (cranium, Plate 6, figures K, N), lower part of the Whittaker Formation, locality C655, Funeral Range, Mackenzie Mountains, District of Mackenzie, Canada.

Other material.—Cranidia, hypostomes, and pygidia very common at locality C655, Funeral Range. Cranidia, hypostomes, and pygidia common at locality H1975, Whittaker Range.

Description.—Cranidium weakly convex (trans. and long.); glabella 90-100% as long as wide, uniformly granular except in the furrows, with gently convex lobes and deep furrows. Occipital ring weakly arched transversely, tapers to a point abaxially. Occipital furrow well-defined. Central lobe weakly swollen and rises only a little higher than bullar lobes, very strongly expanded anteriorly, extends all the way across bullar lobe, narrows strongly backward. Longitudinal furrows sharply defined, die out at posterior of bullar lobe. Bullar lobe short, 30-35% length (sag.) of cranium, much narrower than central lobe opposite eye, circumscribed, weakly convex. L1b long, 15% length of cranium, confluent with L1a. Both are kidney-shaped and prominent above the occipital ring. Preglabellar furrow shallow. Anterior border extremely wide (sag. exsag.), expanding abaxially. Axial furrow strong anteriorly, shallows backward, confluent with S1. Eye ridge broad, finely granular, strong, runs backward and abaxially from anterolateral angle of glabella to palpebral lobe, which is short (15% length of cranium) with midlength opposite S1. Palpebral furrow deep and narrow, runs almost longitudinally from axial furrow and marks off an acute anterolateral angle within the more coarsely granular area of the fixigena. Fixigena convex, slope steeply laterally and backward, almost twice as long (exsag.) abaxially as adaxially. Posterior border short (exs.) adaxially, widens strongly abaxially. Posterior border furrow deep, widens near extremity. Anterior branch of facial suture runs forward and inward along the side of the eye ridge, cuts anterior margin at an obtuse angle; posterior branch curves outward and backward. Prosopon granular; anterior border, eye ridge, and lateral area of posterior border finely granular. A large granule, conspicuous on internal mold, situated at anterolateral extremity of frontal lobe. Granule in A1 position slightly enlarged.

Pygidium 60-65% as long (sag.) as wide. Axis 40% maximum width of pygidium, strongly arched transversely, narrows strongly at 40% of pygidial length from front; postaxial ridge narrow, strongly developed, merging with border. First ring complete. Axial furrow deep anteriorly, shallows backward, well-defined. Pleural lobe moderately convex. First pleura narrow (tr.), extended into free point. Anterior band less swollen than posterior band, marked off by interpleural furrow that dies out at base of free point. Second pleura similarly constructed, but larger and wider (tr.) and expands more strongly abaxially. Posterolateral border swollen and marked off chiefly from anterior band by broad border furrow. Third pleura unfurrowed, area inside border gently swollen and circumscribed by interpleural and border furrows. Posterolateral border broad, weakly defined. Terminal free points as large as second, separated by a narrow V-shaped notch. A much smaller second free point at anterior extremity of third pleurae. Doublure 30% length of pygidium, convex posteriorly, concave anteriorly; anterior margin simple. Terrace ridges fine, closely spaced. Dorsal surface granular adaxial to inner margin of doublure, weakly and sparsely granular abaxially.

Discussion.—Among the named species of the genus, *Hemiarges diadayma* n. sp. most closely resembles *H. leviculus* Bradley (1930, p.

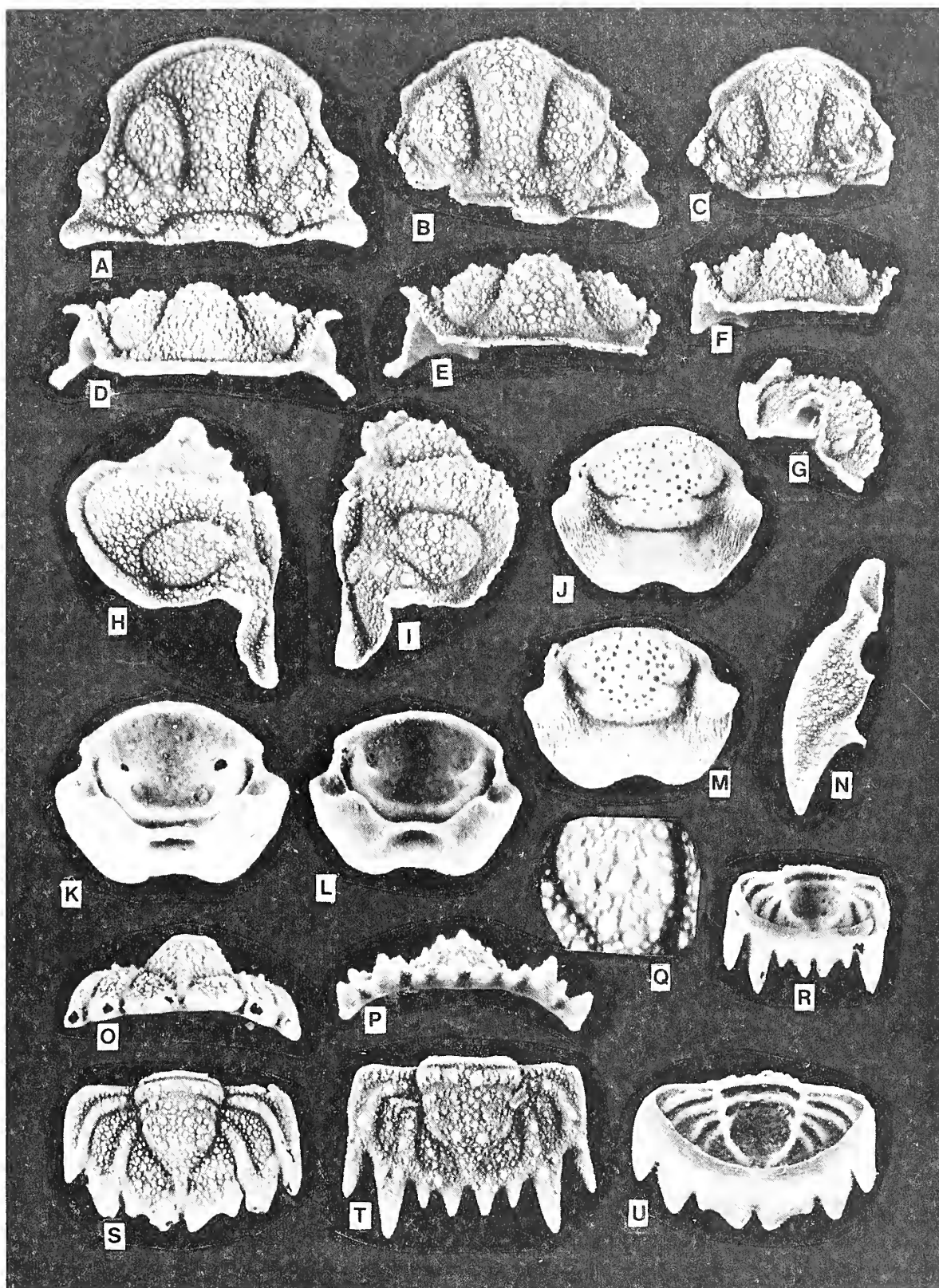


Plate 5. *Hemiargus turneri* subspecies. A, D, H, J, K, N, O, Q, S, U, *H. turneri elassouothos* n. subsp., locality P2038, top of Esbataottine Formation (Blackrivercan), Sunblood Range, Mackenzie Mountains, District of Mackenzie, x11.5; Q, x23. A, D, H, Q, Dorsal, frontal and oblique left lateral views of cranium; Q is enlargement of left bullar lobe, ROM 46082. J, Ventral view of hypostome, ROM 46084. K, Dorsal view of hypostome, ROM 46085. N, Dorsal view of left librigena, ROM 46083. O, S, Posterior and dorsal views of holotype pygidium, ROM 46086. U, Ventral view of pygidium, ROM 48702 (specimen missing). B, C, E, F, G, I, L, M, P, R, T, H. *turneri turneri* Chatterton and Ludvigsen, 1976, Esbataottine Formation (Chazyan), Mackenzie Mountains, District of Mackenzie. B, E, I, Dorsal, frontal, and oblique right lateral views of cranium, x8.5, GSC 43451, locality A125. (B and I illustrated by Chatterton and Ludvigsen, 1976, Pl. 19, figs. 15, 14). C, F, G, Dorsal, frontal, and right lateral views of small cranium, ROM 48703 (specimen missing). L, M, Dorsal and ventral views of hypostome, ROM 48704 (specimen missing). P, T, Posterior and dorsal views of pygidium, x8.5, GSC 43452, locality A125 (illustrated by Chatterton and Ludvigsen, 1976, Pl. 19, figs. 36, 37). R, Ventral view of pygidium, ROM 48705 (specimen missing).

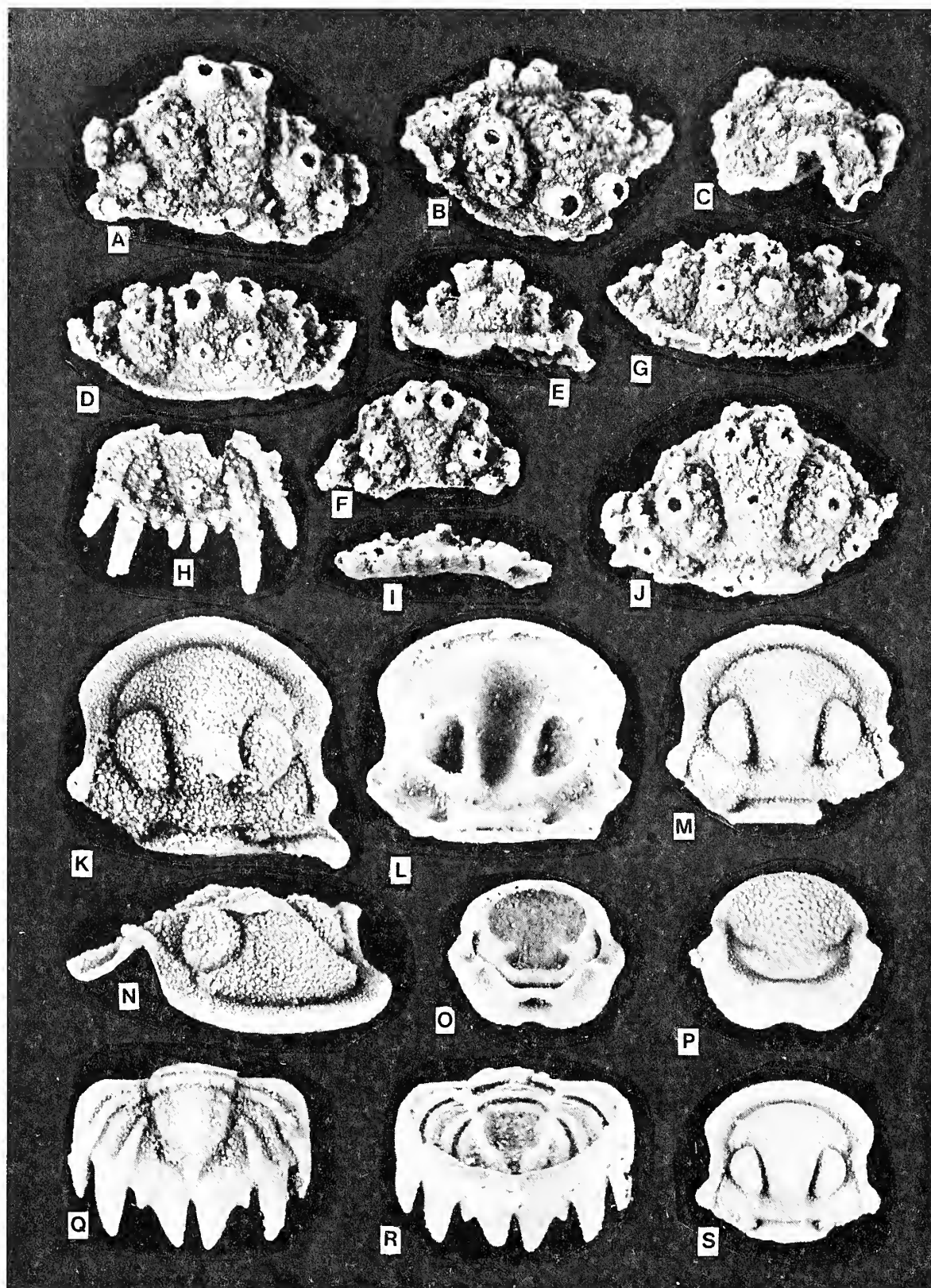


Plate 6. New species of *Hemiarges*. A-J, *H. balanus* n. sp., lower part of Whittaker Formation, locality H1920, Whittaker Range, Mackenzie Mountains, District of Mackenzie, x11.5. A, B, D, Dorsal, oblique right frontal, and frontal views of holotype cranidium, ROM 46087. C, G, J, Left lateral, frontal, and dorsal views of cranidium, ROM 46090. E, F, Frontal and dorsal views of cranidium, ROM 46088. H, I, Dorsal and posterior views of pygidium, ROM 46089. K-S, *H. diadayma* n. sp., lower part of Whittaker Formation, locality C 655, Funeral Range, Mackenzie Mountains, District of Mackenzie, x11.5. K, N, Dorsal and oblique right frontal views of holotype cranidium, ROM 46091. L, Ventral view of cranidium, ROM 46092. M, Dorsal view of cranidium, ROM 46093. O, Dorsal view of hypostome, ROM 46094. P, Ventral view of hypostome, ROM 46095. Q, Dorsal view of pygidium, ROM 46096. R, Ventral view of pygidium, ROM 46097. S, Dorsal view of cranidium; note protuberant L1a, ROM 46098.

271, Pl. 29, fig. 22) from the Kimmswick Limestone of Illinois in the broad anterior border and weak convexity. However, the bullar lobes are much smaller in the new species, and the prosopon is distinctive.

Sparse material from the Whittaker Formation at locality H1920 in the Whittaker Range, identified as *Hemiarges* sp. aff. *H. diadayma*, is closely similar to Funeral Range material but differs in the broader bullar lobes and coarser prosopon, which is particularly apparent on the anterior border (specimen ROM 46099). There is no enlarged tubercle on the anterolateral angle of the frontal lobe of these specimens.

Etymology.—*diadayma* n. sp., a royal headdress (Gk.).

Acknowledgments

We are grateful to the following for the loan of specimens in their charge: T. Bolton, Geological Survey of Canada, Ottawa; F. Collier, National Museum of Natural History, Washington, D.C.; and S. Lidgard, Field Museum of Natural History, Chicago. V. Poulsen of the University of Copenhagen kindly provided casts of Troedsson's types from the Cape Calhoun Formation, Northern Greenland. I. Steins prepared the figures. We express our thanks to F. Shaw and G. Edgecombe for their comments and suggestions on earlier versions of this paper. The Royal Ontario Museum supplied \$225 toward publication of this report.

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Isostrophically coiled shells: *Porcellia* and the Bellerophontoidea

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Abstract

Porcellia prolatatora n. sp., a pleurotomarioidean gastropod from the Middle Devonian Rogers City Limestone in the northeastern Michigan Basin, is described. The unusual discoidal shell form prompted an analysis of the presumed shell-righting behavior and a comparison to the inferred shell-righting behavior of the Bellerophontoidea, among which the Tropicodiscinae have a strong morphologic similarity to *Porcellia*. The conclusion is that the shell-righting behavior supports the classification of mollusks with enigmatic bellerophontiform shells in the Class Gastropoda rather than in the Monoplacophora.

Introduction

A new species of the gastropod genus *Porcellia* Léveillé (Prosobranchia, Pleurotomarioidea) was found in the Middle Devonian Rogers City Limestone from the northeastern portion of the Lower Peninsula of Michigan. *Porcellia* is an unusual gastropod; although its embryonic whorls are orthostrophic and it is obviously a pleurotomarioidean, its adult whorls approximate isostrophic coiling. This gives the adult conch a flattened discoidal form unlike any living prosobranch. In this way, it is convergent upon the Bellerophontoidea, particularly the genus *Tropicodiscus* Meek and Worthen.

The Rogers City Limestone crops out in the northeastern part of the Michigan Basin for about 50 km from Middle Island near Rockport Quarry to just west of Rogers City, Michigan, where it disappears beneath glacial cover. Much of this part of Michigan has extensive glacial drift, and the Rogers City Limestone is visible in only about a dozen different localities along its 50 km outcrop belt. However, the chemical purity of the limestone is so high that two large limestone quarries have been opened to extract it. The specimens studied in this report all come from the Calcite Quarry of Michigan Limestone Operations of the U.S.X. Corporation at Calcite, south-southeast of Rogers City, Michigan ("the world's largest limestone quarry"). This is an impressive operation that provides over 10 km of continuous exposure in the walls of the quarry.

Lithology and general paleontology

The Rogers City Limestone is about 21 m thick and has been subdivided

into six units (Ehlers and Kesling, 1970). Units 1 and 2 are dolomitic and have been interpreted as penecontemporaneous dolostones that accumulated in a supratidal environment (Linsley, 1973). Units 3 and 4 are fine-grained limestones with a depauperate fauna and have been interpreted as back-reef lagoonal environments. Units 5 and 6 (the upper 15 m of the limestone) are a very coarse-grained limestone with a very diverse fauna dominated by corals, stromatoporoids, bryozoans, and gastropods, and have been interpreted as a reef.

Porcellia has been found so far only in unit 1, the dolostone. It is a very rare member of the fauna, and only four specimens (plus two specimens provisionally assigned to the species) are known from the collections of Colgate University, the University of Michigan, and the U.S. National Museum. Fossils are relatively rare in unit 1, and are found either in pavements composed of the brachiopod *Emanuella* or in size-sorted shell hashes with a diverse faunal composition. *Porcellia* is found in the shell hashes and is presumed to have lived in the quiet water just offshore. It is an element of a diverse fauna that includes *Hypomphalocirrus rugosus* Linsley, *Straparollus* (*Straparollus*) *cottrelli* Linsley and Yochelson, *Mastigospira ingens* LaRocque, *M. intermedia* LaRocque, *Actinopterella calliotis* LaRocque, *A. peninsularis* LaRocque, *Leptodesma furcistriata* LaRocque, and *Limoptera* (*Myalinodonta*?) *migrans* LaRocque. Undescribed bellerophontiform species, tentaculitids and tubular shells doubtfully assigned to *Dentalium* are also associated in this fauna.

The most striking aspect of the fauna of the Rogers City Limestone is that it bears little similarity to the faunas of the underlying Dundee Limestone or the overlying Traverse Group. The Dundee and Traverse faunas both show strong affinities to the Appalachian Basin and can be correlated with counterparts in the New York section. The fauna of the Rogers City Limestone correlates biostratigraphically with the "*Stringocephalus* fauna" of Germany, Manitoba, and western North America (even though the brachiopod *Stringocephalus* has not been found in the Rogers City Limestone). (For further discussion, see Cooper and Phelan, 1966, and Linsley, 1973.)

Systematic paleontology

Class GASTROPODA Cuvier, 1797

Subclass PROSOBRANCHIA Milne-Edwards, 1848

Order ARCHAEOGASTROPODA Thiele, 1925

Suborder PLEUROTOMARIINA Cox and Knight, 1960

Superfamily PLEUROTOMARIOIDEA Swainson, 1840

Family PORCELLIDAE Broili, 1924

Genus PORCELLIA Léveillé, 1835

Type species.—*Porcellia puzo* deKoninck, 1883

PORCELLIA PROLATATORA n. sp.

Figure 1A-D, E?, F?

Diagnosis.—Species of *Porcellia* with orthostrophic shell that becomes approximately isotrophic in the adult volutions; strong elongate nodes appear in the third whorl and increase in size isometrically towards the aperture; fourteen to seventeen nodes per half-volution.

Etymology.—Derived from the Latin *prolatus* (elongate) and *torus* (swelling).

Description.—Dextral discoidal shells of about four volutions; form converges on isotrophism in adult whorls; nepionic and neonic whorls poorly known but seemingly orthostrophic; adult whorls with well-developed nodes seemingly asymmetrically offset on top and bottom of shell; aperture presumably with a deep slit that generates a selenizone that is flush with the outer whorl face. Upper whorl face poorly known, but the upper suture is seemingly deeply incised, and the upper whorl

face is gently rounded from suture to selenizone; basal whorl face well-known and gently rounded from selenizone to basal suture in mature whorls. As nodes develop in the mature portion of the conch, they give the appearance of a nodose shoulder on the base. Based on growth lines, the aperture is tangential with the growth lines curved backward obliquely from the basal suture to the inner margin of the nodes, where they continue with a gentle forward convexity across the nodes to the selenizone. Slit unknown, but selenizone flush with the outer whorl face; slit narrow and inferred as deep, possibly extending as much as half a volution. Ornamentation consists of nodes in the adult volutions, presumably asymmetrically disposed on the top and bottom of the shell; early whorls smooth with nodes beginning to appear on about the third volution and becoming progressively larger on the adult whorl; nodes evenly spaced with approximately fourteen to seventeen nodes per half-volution; nodes gently crescentic in shape and collabral with their concave side facing the aperture.

Largest specimen measures approximately 1.4 cm in diameter.

Discussion.—The description is based on a study of four specimens plus one very immature specimen that has been provisionally assigned to this species. The four adult specimens are all molds of the base of the

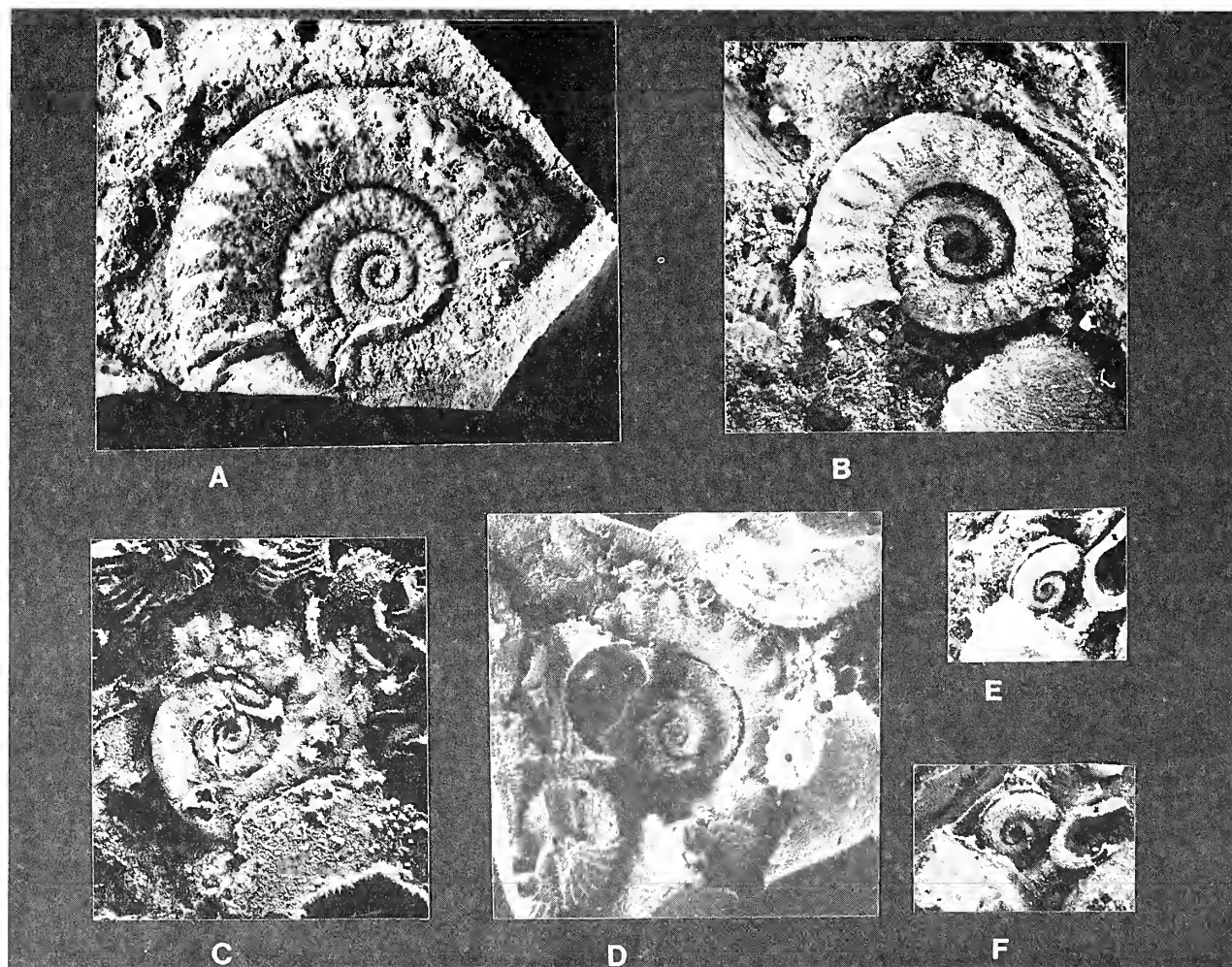


Figure 1. *Porcellia prolatatora* n. sp. All figures x4. A, Holotype UMMP 66052. Basal view of latex cast showing the elongated, prominent nodes that increase in size toward the ultimate volution. B, Paratype UMMP 22367. Basal view of latex cast showing orthostrophic nature of nuclear whorls. C, Paratype UMMP 66053. Basal view of latex cast of a poorly preserved specimen that illustrates the beginning of strongly developed nodes. D, Paratype UMMP 66054. Basal view of latex cast with strongly developed nodes on ultimate whorl. The penultimate whorl is a steinkern in the mold of the specimen. E, F, Apical view of UMMP 66055, a specimen that is assigned to *P. sp. cf. P. prolatatora* n. sp. This is the only specimen that exhibits the apical side of this species. The feature apparent on the periphery of the whorl is interpreted herein not as the selenizone, but as the suture of a broken subsequent volution.

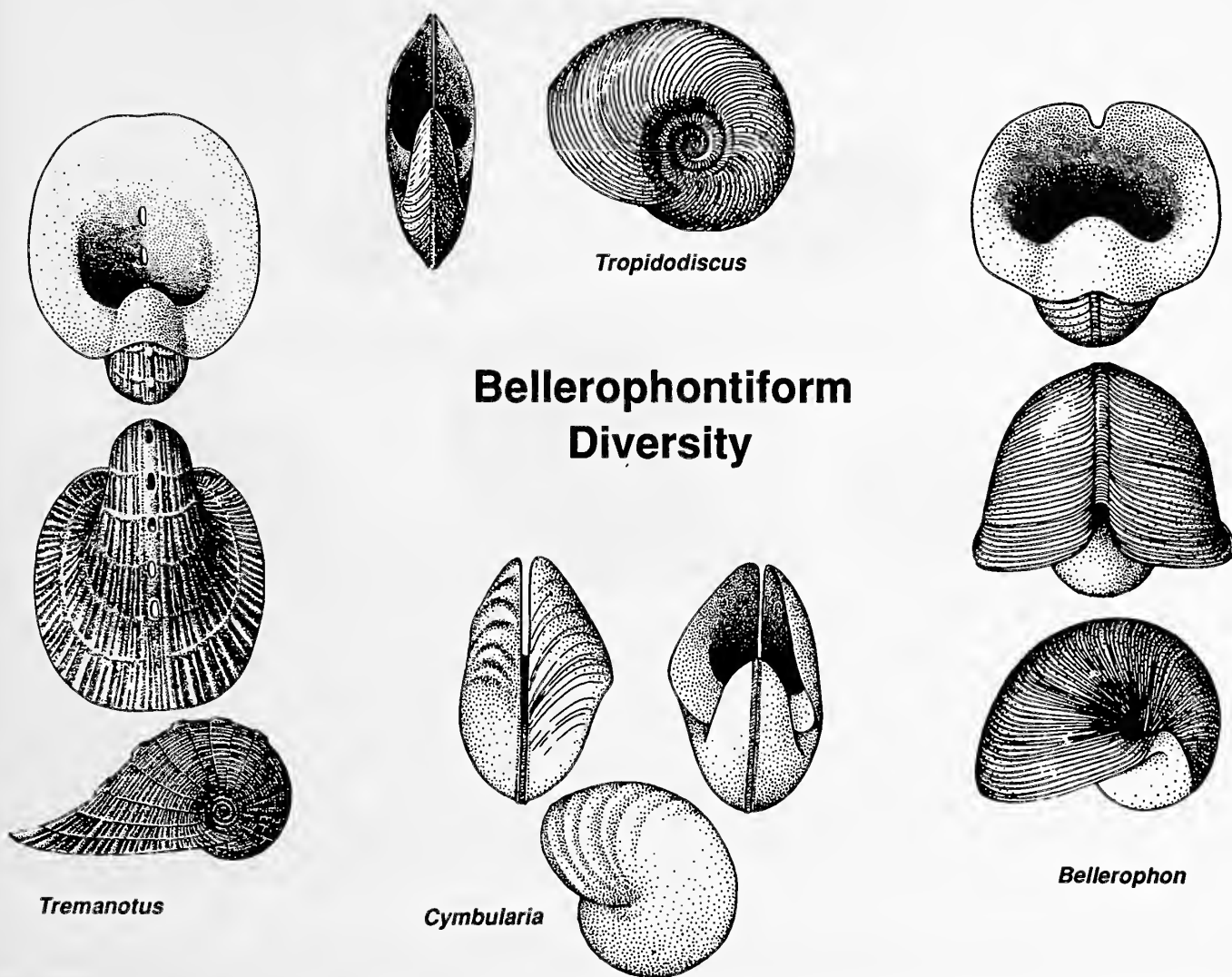


Figure 2. Bellerophontiform diversity. Three major morphologies occur in bellerophontiform shells. These morphologies are typified by *Bellerophon* (a spherical shell), *Tropidodiscus* (a flattened discoidal shell), and *Tremanotus* (a bellerophontiform shell with rapidly expanding shell and highly explanate aperture). Also figured is *Cymbularia* (an asymmetrical shell). Line drawings taken from Knight et al. (1960, Figs. 95, 97, 102).

shell, and on none of the specimens is a selenizone evident. In addition, one specimen figured by Radabaugh (1942, Pl. 11, fig. 3-4) is a complete cast that shows the nature and position of the selenizone. This specimen was assigned to *P. manitobensis* by Radabaugh, an incorrect assignment that is discussed below. This specimen was unavailable for analysis in this study. The provisionally identified specimen described below is very immature and does not show the nodes characteristic of the adult conch because it is an impression of the apical side of the shell (Figure 1E, F).

Porcellia prolatatora n. sp. can be distinguished from *P. puzo* (Léveillé, 1835) by the elongated nodes of the new species and its lack of a reticulate ornamentation that occurs prominently in *P. puzo*. The new species can be distinguished from *P. manitobensis* (Whiteaves, 1892), *P. striata* (Goldfuss, 1844), *P. shingensis* (Guo, 1982), and *P. parva* (Miromova, 1985) in that all of the latter species have an ornamentation that features striations and lack nodes. Two other species of *Porcellia* have about fourteen to seventeen nodes per half-volution; these include *P. puzoidea* (Hayasaka, 1955) and *P. lingshuensis* (Pan, 1985).

Porcellia prolatatora n. sp. is distinguished from all of these species by the fact that its nodes do not appear until the third volution, and then increase in size isometrically to the adult whorl. *Porcellia puzoidea* has nodes that are present immediately after the first volution and maintain a relative size. In *P. lingshuensis*, the nodes decrease in relative size so that the last two-thirds of the adult whorl are smooth. All specimens are external molds taken from unit 1 of the Rogers City Limestone.

Types.—Holotype UMMP 66052; paratypes UMMP 22367, 66053, and 66054; figured specimen UMMP 66055.

Analysis

Isostrophic shells are easily distinguished by their bilateral symmetry. The analysis of such shell forms is of concern to many paleontologists because the conchs of many systematic groups are convergent on this shape (cephalopods, fresh water and marine gastropods, monoplacophorans). In the past, the reconstruction of the mollusk that inhabited

PROPOSED SHELL RIGHTING FOR *PORCELLIA*— RIGHT SIDE SCENARIO

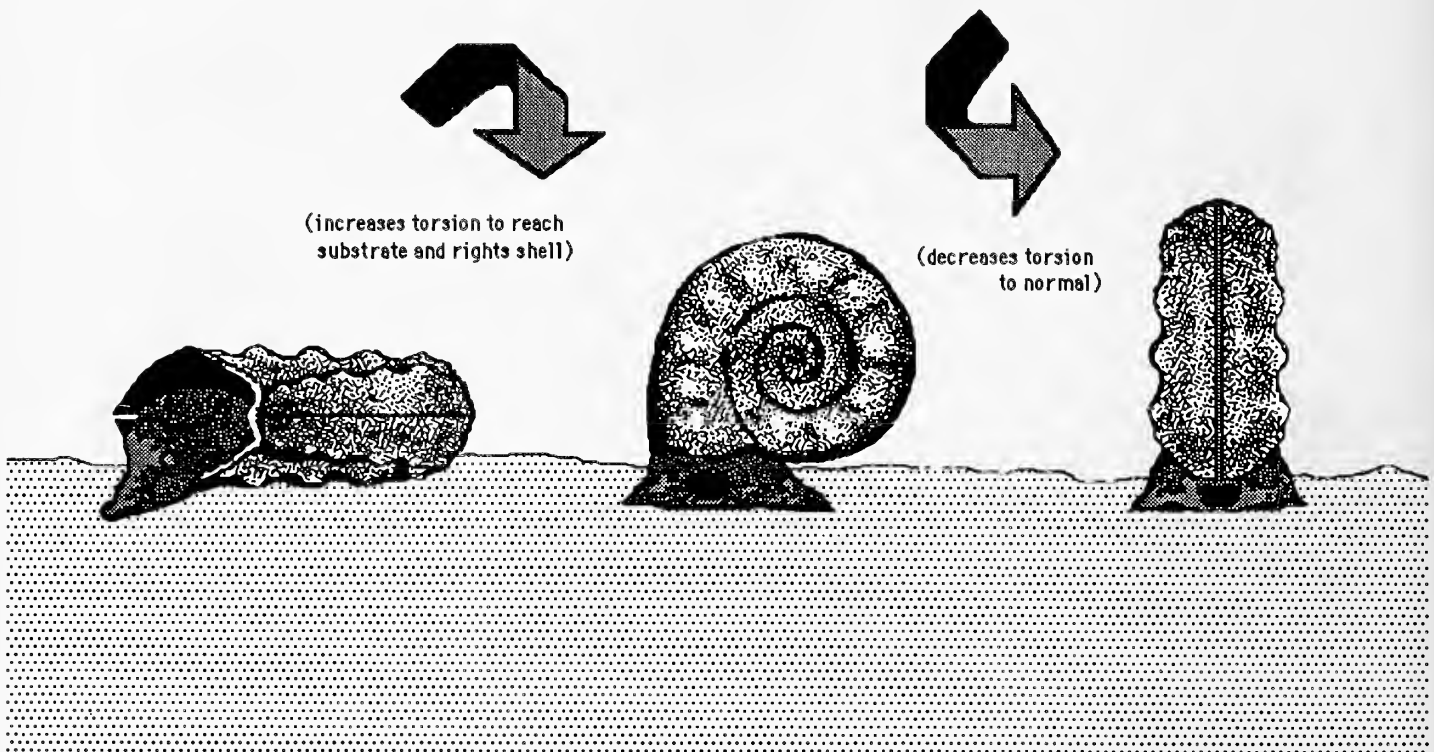


Figure 3. Proposed shell-righting for *Porcellia*—right side scenario. In this model, *Porcellia* has fallen to its right side after withdrawal into its discoidal shell. To right the shell, the animal must undergo a visceral rotation to increase its effective torsion past that of its normal crawling condition in order to reach the substrate with its foot. Once anchored in some way, the animal pulls the shell upright by contracting its pedal retractor. The shell is then rotated to decrease the effective torsion to normal.

isostrophic shells has proven to be quite a challenge, and this has often led to a classification that is either incorrect or debatable. The particular history of the isotrophic gastropod *Porcellia* is just one example. It was twice described as a new genus of cephalopod (see White and St. John, 1867; Miller et al., 1952). This suggests some of the uncertainty paleontologists face when dealing with isostrophism.

The largest group of non-septate isostrophic forms in the fossil record is the Bellerophontoidea, and it is around this group that the so-called "Bellerophont Controversy" has revolved (see Harper and Rollins, 1982). Over the years, various arguments have risen to place them in either the Gastropoda or the Monoplacophora. One major distinction is how the animal carried its shell, in addition to significant differences in soft-part anatomy (torted or untorted).

In this paper, the term "bellerophontiform" will be used to refer to all isostrophic non-cephalopod mollusks without inference of systematic position. This usage is applied because it is apparent that the problematic forms are not currently restricted to one taxonomic group.

The Monoplacophora are represented today by one living family (Neopilinidae). They are distinguished by unique musculature, pseudometamerism, lateral mantle cavity, and short bodies that lack any clearly defined head. If reconstructed as a monoplacophoran, the coils of a bellerophontiform shell would be carried anteriorly. The Gastropoda, a much more common group today, are characterized by torsion. Torsion means that the body has undergone a twisting that

rotates the shell and brings the mantle cavity to the anterior early in larval ontogeny. Gastropods commonly have a longer body than monoplacophorans, and have a well-developed head that is separated from the body by a neck. In bellerophontiform gastropods, torsion would be 180° and the coils of the isostrophic shell would be carried posteriorly. Knight (1952) placed the bellerophontiforms in the Gastropoda on the basis of shell form and reconstruction of inhalant/exhalant current hydrodynamics (see also Peel, 1974; Linsley, 1978).

Horný (1965) discovered characteristic muscle attachment scars in an isostrophic shell of *Cyrtolites* (Conrad, 1838) that led to its interpretation as a monoplacophoran. This, in part, has led some workers to consider all bellerophontiform mollusks as referable to the Monoplacophora (Runnegar and Pojeta, 1974; Runnegar and Jell, 1976; Salvini-Plawen, 1979). The interpretation of such evidence as muscle scars has played an important part in the latest episode in the bellerophont puzzle (Knight, 1947; Yochelson, 1967; Runnegar and Pojeta, 1974; Runnegar and Jell, 1976; Peel, 1976, 1980, 1986). These scars indicate points of muscle attachment on the shell interior; they are usually interpreted as denoting the position of the pedal retractor muscles that are responsible for the withdrawal of the body into the shell. These scars appear as raised ridges on the surface of the steinkern.

In cap-shaped monoplacophorans and in Horný's (1965) coiled specimens of *Cyrtolites*, muscle scars are found in multiple pairs and occupy bilaterally symmetrical positions close to the aperture. Most

PROPOSED SHELL RIGHTING FOR *PORCELLIA*— LEFT SIDE SCENARIO

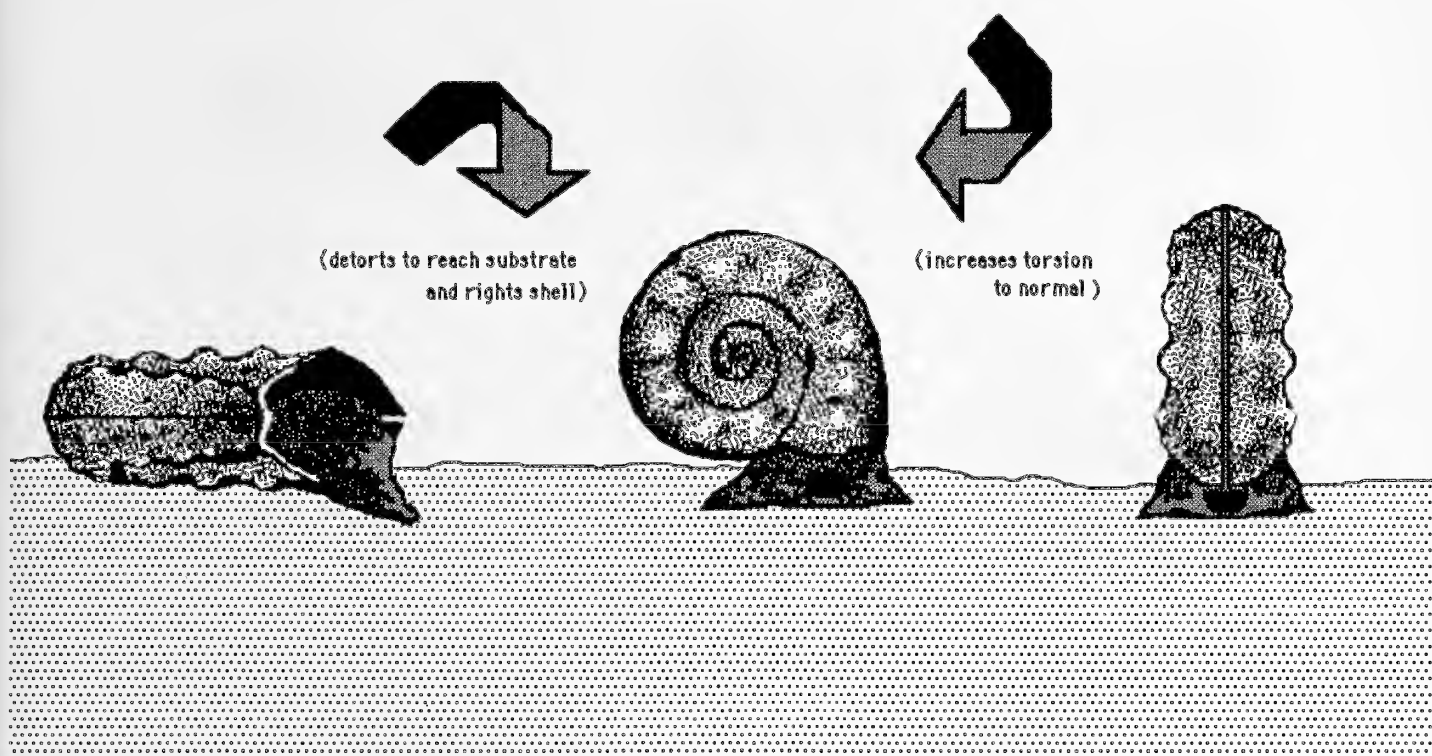


Figure 4. Proposed shell-righting for *Porcellia*—left side scenario. After falling on its left side and withdrawing into its shell, the animal undergoes a visceral rotation to decrease its effective torsion from its normal living position to reach the substrate. Once a firm purchase has been gained, the animal rights the shell and rotates to increase its effective torsion back to its living position.

gastropods, however, show a single muscle scar farther back in the shell. The subsequent discovery of paired muscle scars as far back as three-quarters of a revolution from the aperture in the shells of some bellerophonitiforms has been used as conclusive evidence both of their monoplacophoran affinities (Runnegar, 1981) and for their classification as gastropods (Peel, 1980). This disagreement about systematic affinity has led to uncertainty about the utility of a classification based primarily on muscle scars (Peel, 1986; Harper and Rollins, 1982).

Shell-righting and withdrawal

Porcellia becomes interesting in this context because it displays many of the characteristics of the Bellerophonitoidea, even though it is unquestionably a gastropod. Its nuclear whorls exhibit the asymmetrical coils of a typical dextral gastropod (see Knight, 1941, Pl. 38, figs. 6a-e). In the adult stage, this growth mode is replaced by one that approximates isostrophism. This results in its distinct discoidal form. The anal slit found in *Porcellia* is so deep that the anus has a posterior position even though the shell is torted. In addition, it is one of the few known gastropods that produced a symmetrical pair of muscle scars, rather than an asymmetrical pair or a single scar (Peel, 1986). In coiling morphology as well as inferred anatomy, *Porcellia* is a suitable analogue with which to approach the enigma of the Bellerophonitoidea. The morphology of *Porcellia*'s conch, with discoidal form, deep slit, and deep paired muscle scars, bears a close resemblance to that of the bellerophonitoidean *Tropidodiscus*.

A new approach to the enigmatic bellerophonitiform groups is an

attempt to relate the varied morphologies in this group to the shell-righting and withdrawal behavior of the animals. This approach encompasses how the animal would pull its head and foot back into its shell during withdrawal, how the shell would rest on the substrate when the animal was retracted, and how it would regain its normal shell orientation during shell-righting behavior. To undertake such an analysis is somewhat problematical, because there are no living bellerophonitiform mollusks. The planispiral, isostrophic prosobranch *Porcellia* is extinct, but it serves as a link between the morphology of the extinct bellerophonitiforms and the righting and withdrawal behaviors of modern gastropods. Linsley's unpublished studies of withdrawal and righting behavior in living gastropods based on time-lapse movies allow some generalizations to be made.

A gastropod withdraws primarily as a defensive reaction in response to a predator or adverse environmental conditions. If an animal is disturbed, it undergoes an initial rotation of the body in the direction opposite from its ontogenetic torsion. This may be regarded as "effective detorsion". It then pulls the body into the shell by use of the pedal retractors. The head is withdrawn first into the most protected position; the foot is pulled in afterwards. The gastropod foot actually folds upon withdrawal, with the metapodium rotating 180° so that the previously dorsal operculum (if present) seals the aperture of the shell.

The most obvious aspect of righting behavior is the apparent "trepidation" with which righting is frequently approached. Even so, gastropods seem able to adapt easily to the varying conditions that accom-

Shell Orientation Upon Withdrawal

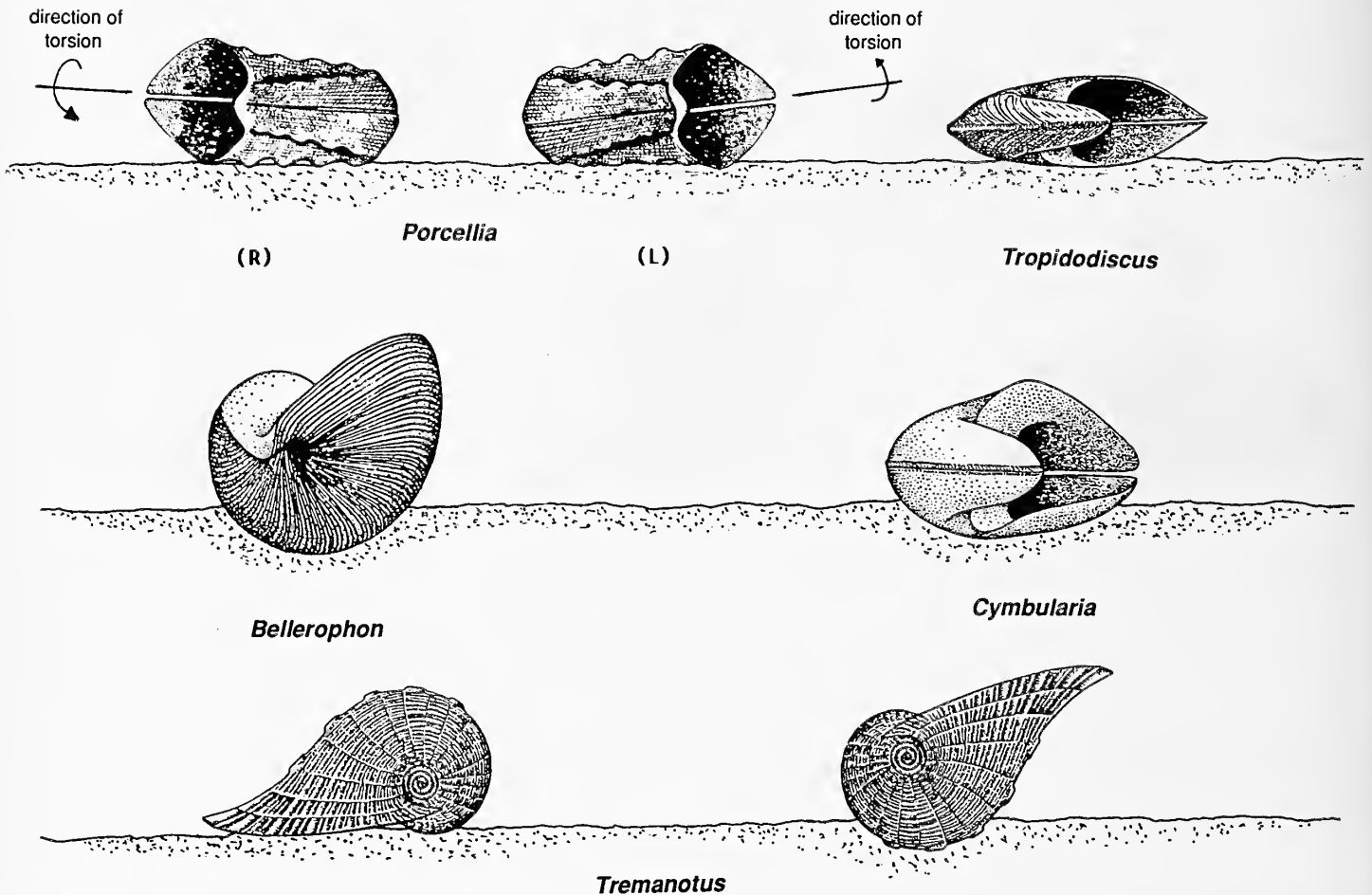


Figure 5. Shell orientation of bellerophontiform shells upon withdrawal. *Porcellia* and the three characteristic bellerophontiform shells are shown as they would be oriented upon withdrawal, with the shell resting against the substrate. *Porcellia*, as *Tropidodiscus*, would fall to either side upon withdrawal (the directions for initiating righting, both with and against the living position torsion, are indicated). *Bellerophon* would presumably roll with the wave action. *Tremanotus* would most likely wind up with its wide, stable aperture against the substrate, although the reverse case is also figured. If overturned, the asymmetrical shell of *Cymbularia* would preferentially lie with its flattened left side against the substrate. This asymmetry, a seemingly enigmatic feature of *Cymbularia*'s morphology, can be understood if it is related to the righting behavior in *Busycon* and *Porcellia*. *Busycon*'s preference to decrease effective torsion by visceral rotation, and the inferred effective detorsion of *Porcellia* if its left side comes to rest against the substrate, can be applied to reconstruct *Cymbularia* behavior. If the soft parts were withdrawn, the animal would lie on its left side, and this would confer an understandable advantage in shell-righting if its soft parts were tort. This evidence speaks for a gastropod classification of *Cymbularia*. Line drawings taken from Knight et al. (1960, Figures 95, 97, 102, 129).

pany righting. Strombiids, lamiids, and trochiids have developed the unique variant behavior of righting the shell by thrusting the operculum against the substrate, thus "kicking" the shell over. In general, though, some more basic patterns are apparent. Most often, the gastropod protrudes its foot from the region on the aperture nearest the substrate in order to right its shell. This implies that the animal can distinguish this region of the aperture. If probing by the foot determines that the substrate is hard, the animal grips the substrate with its foot and gains enough leverage to pull the shell upright. If the substrate proves to be soft, the animal simply extends its foot even farther and probes into the substrate for leverage, or even extends the foot under the shell to provide a suitable surface for righting. This behavior sequence assumes that the animal moves by muscular contraction and not cilia (see Miller, 1974). In all cases, the shell is rotated after righting into the normal car-

rying position in order to compensate for the original visceral rotation at the onset of withdrawal.

Discussion

On the basis of the righting behavior of modern gastropods, there appear to be three general morphologies of bellerophontiform shells that would have distinct righting patterns (Figure 1). These are typified by *Bellerophon* Montfort (a spherical shell), *Tropidodiscus* (a discoidal shell), and *Tremanotus* Hall (explanate). Additionally, there is the infaunal interpretation of *Euphemites* Warthin (Harper and Rollins, 1985), but presumably it would behave much as genera with a similar spherical shape if the animal was withdrawn and the shell was at the surface of the substrate.

Porcellia, following withdrawal into its discoidal shell, would fall to

either side. It is important to remember at this point that, because *Porcellia* was a dextral gastropod, its living position incorporated within it an ontogenetic 180° counter-clockwise rotation of its shell. If the animal fell on its right side (Figure 3), *Porcellia* must have momentarily increased the effective torsion by 90° to reach the substrate with its foot, which would then be anchored to enable the animal to crawl under the shell. Once the shell was upright, it would be rotated clockwise; this reduced the effective torsion from some 270° to the normal 180°.

A marked tendency to avoid increasing the effective torsion of the visceral mass past that of ontogenetic torsion (when possible) was observed in stop-action films of the gastropod *Busycon* Röding. The animal, when confronted by the corners of its aquarium, is in a difficult position because its long siphon makes turning impossible, and, as in most gastropods, the nature of its locomotion does not allow it to go backwards. To free itself, *Busycon* withdraws into its shell, turns its body 180° inside the shell, and comes out facing the other way. It is then able to proceed out of the corner, and undergoes a 180° rotation in order to return to its normal life position. When rotation occurs within the shell, *Busycon* always chooses to decrease the normal 180° effective torsion of its living position, rather than to increase it through visceral rotation.

Now, if *Porcellia* fell to its left side (Figure 4), the animal would necessarily undergo an effective detorsion to reach the sediment, right the shell, and increase the effective torsion to normal. This behavior would be similar to that observed in *Busycon*.

Porcellia was certainly able to right itself regardless of its position on the substrate. However, it may have been able to right the shell more easily after falling on its left side rather than on its right side.

The shell-righting behavior of the bellerophonitiforms can now be interpreted (Figure 4). *Tropidodiscus*, if interpreted as a monoplacophoran, would not have exhibited this bilateral difference in shell-righting behavior. However, if it is interpreted as a gastropod because of its deep (one-half volution) slit, its righting behavior would presumably be analogous to that of *Porcellia*.

Bellerophonitiform species with spherical conchs (such as *Bellerophon*) would roll about as a result of current or wave action after withdrawal of the body. If the Monoplacophora are regarded as short-bodied, shallow-muscled animals that lack a neck, they would seemingly have a most difficult time reaching the substrate if overturned. However, if the concept of the Monoplacophora is expanded to include deep-muscled, more elongate organisms, then they may be presumed to have a righting behavior analogous to that of gastropods. It is important to note that Figure 5 shows the worst-case scenario, and *Bellerophon* conchs would probably be rolled on their side or onto their aperture just as often as they would come to lie with their aperture up. Modern gastropods, which seem eminently adaptable to a number of modes of righting, would have no problem righting a spherical conch.

Of special interest among the relatively spherical bellerophonitiforms is the asymmetrical shell of *Cymbularia* Koken. The left side has become flattened in this form. No apparent explanation for this asymmetry has yet been proposed. However, if the hypothesized preference in *Porcellia* for effective detorsion during the substrate-grabbing phase of righting is attributed to *Cymbularia* as well, this asymmetry may be understood from a functional viewpoint. The asymmetry of the flattened form would mean that the shell would more frequently rest on its left side after withdrawal. This would reduce the chance of increasing effective torsion to 270° during righting. This asymmetry is consistent with the classification of *Cymbularia* in the Gastropoda. If the animal is interpreted as a monoplacophoran, the asymmetry remains unintelligible. It should be noted that other asymmetrical bellerophonitiform shells

(*Stachella* Waagen and *Ptychosphaera* Perner) pictured in *The Treatise on Invertebrate Paleontology* are both illustrated as being flattened on the left side, as is *Cymbularia*. However, *Stachella*'s asymmetry has been challenged by Yochelson (1960, p. 231), and *Ptychosphaera* was not reexamined for this report to ascertain whether the asymmetry is real or a preservational artifact.

The explanate conch of *Ptomatis* Clarke has been interpreted as having shallow muscle attachments (Rollins et al., 1971). If this interpretation is correct, the short body of the monoplacophoran would be at a distinct disadvantage if this rapidly expanding conch were ever overturned. Peel (1972) has described the muscle attachment scars in other explanate forms. In *Ptomatis*, the muscles are inferred to be attached to the top of the inductural callus and close to the aperture. The paired muscle scars described by Peel (1972) in *Salpingostoma* Roemer, another explanate bellerophonitiform, are a quarter-volution from the aperture. In *Tremanotus*, Peel (1972) observed scars a full volution back from the aperture. These varying positions would seem to correspond to the relative depth of the exhalant opening in each genus. In *Ptomatis*, this re-entrant appears as only a short sinus, whereas in *Salpingostoma* it forms a tremata positioned a quarter-volution from the aperture. *Tremanotus* has a series of tremata extending three quarter-volutions from the aperture. Thus for these forms that have more deeply placed muscle scars, it is problematic to infer their systematic position from inferred righting behavior. However, in some instances, systematic affinity of these forms has been proposed solely on the presence of tremata (Peel, 1972).

Conclusion

Definitive criteria for the systematic classification of isostrophic shell forms are still not available, but the insight gained from an examination of the probable shell-righting and withdrawal behavior of bellerophonitiforms adds another aspect to the argument for at least some of the Bellerophontoidea as members of the Gastropoda.

Acknowledgments

This research was aided by a Grant-in-Aid of Research from Sigma Xi; a grant from Colgate University, Division of Natural Sciences; and the kind assistance of D. Fisher and the University of Michigan Museum of Paleontology; E. Yochelson, USGS (retired); B. Glenister, University of Iowa; D. Erwin, U.S. National Museum; R. Riman, Colgate University; and R. Orloski and D. Linsley, University of Pittsburgh.

Manuscripts were reviewed by D. Erwin, U.S. National Museum; P. Signor, University of California, Davis; and E. Landing, New York State Geological Survey, who provided many helpful insights. We extend our deep appreciation to D. Curtis for her indefatigable help in preparing the manuscript. Colgate University supplied \$750 toward publication of this report.

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Proterozoic–Cambrian boundary trace fossils: Biostratigraphic significance of *Harlaniella* in the Lower Cambrian Wood Canyon Formation, Death Valley, California

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Abstract

Earlier reports have indicated that the ichnogenus *Harlaniella* Sokolov, 1972, is restricted to sediments of a late Vendian age (e.g., Palij et al., 1979; Crimes, 1989). The only ichnospecies previously assigned to the ichnogenus, *H. podolica*, has been employed to define a terminal Proterozoic zone in Newfoundland, at one of the candidate sections for designation as the global stratotype for the Proterozoic–Cambrian boundary. Recent discoveries in the southwestern Great Basin of North America extend the range of the ichnogenus to the middle Early Cambrian. A new species, *Harlaniella confusa* n. ichnosp., is reported herein from the upper member of the Lower Cambrian Wood Canyon Formation of the southwestern Great Basin (*Fallotaspis*, *Nevadella*, and *Bonnia–Olenellus* Zones). The new trace differs from the reported morphology of the genotype species, *H. podolica* Sokolov, 1972, in several critical respects but shares the rope-like form characteristic of the ichnogenus.

Introduction

Definition and correlation of the Proterozoic–Cambrian boundary has proven to be a persistent problem in biostratigraphy. Sub-trilobite, Cambrian shelly fossils are provincial and have notoriously long ranges; thus their utility in biostratigraphic correlations is limited (e.g., Landing et al., 1980, 1989; Landing, 1988; Brasier, 1989; Bengtson et al., 1990). The distribution of shelly fossils is also biased severely by taphonomic and paleoecological controls (Mount and Signor, 1985, 1992; Landing et al., 1989). Although body fossils generally have been the preferred vehicle for defining the boundary (e.g., Cowie, 1978, 1985) and for biostratigraphic correlation within the Lower Cambrian, these and other problems limit biostratigraphic resolution. Furthermore, shelly fossils are not useful in defining Proterozoic strata because only one skeletogenous organism is known from the Proterozoic (excluding the latest Proterozoic (?) Nemakit-Daldyn fauna of the Siberian Platform and coeval fossils elsewhere, which are likely Cambrian in age). The tubular to conical, calcareous fossil *Cloudina* Germs, 1972, is apparently restricted to the Proterozoic (Grant, 1990). (S.W.F. Grant considers *Sinotubulites* Chen, Chen, and Qian, 1981, to be a junior synonym of *Cloudina* and places species assigned to *Sinotubulites* within the latter genus.) *Cloudina* is known from Proterozoic strata on several continents (Germs, 1972; Conway Morris et al., 1990; Grant, 1990) and is only doubtfully reported from the Cambrian (Yochelson and Herrera,

1974; see Grant, 1990). However, *Cloudina* is an uncommon fossil, which limits its biostratigraphic utility. Ichnology could provide the long-sought means to resolve this problem (Seilacher, 1956; Narbonne et al., 1987; Crimes, 1989; Landing et al., 1989).

The critical issue in the use of fossil traces to define any stratigraphic boundary is the reliable stratigraphic distribution of the traces. Unlike body fossils, traces reflect the behavior of organisms and are not necessarily related to a particular taxonomic group (e.g., Ekdale et al., 1984). The distributions of traces are often facies-restricted, as are many body fossils. However, late Proterozoic and Early Cambrian traces were apparently less facies-specific than their later counterparts (Crimes and Anderson, 1985). Many traces have exceedingly long ranges (e.g., *Skolithos*), which reflect extended stereotypic behavior through time. It must be absolutely certain that the ranges of ichnotaxa are temporally restricted if particular fossil traces are to be effective biostratigraphic tools.

There are a number of Proterozoic ichnotaxa that are not recorded from Cambrian strata. Crimes (1989) identified seven genera that are apparently restricted to the Proterozoic (*Bilinichnus*, *Harlaniella*, *Intrites*, *Nenoxites*, *Palaeopascichnus*, *Vendichnus*, and *Vimenites*). In principle, the presence of these ichnogenera could be used to recognize Proterozoic strata. In practice, Proterozoic ichnofossils permit biostratigraphers to identify strata that must lie below any proposed boundary, rather than relying upon an absence of data to define the Proterozoic. Such a use of Proterozoic ichnofossils ensures that further discoveries of shelly fossils do not perpetuate the continued downward migration of the boundary (Narbonne et al., 1987). Unfortunately, the ichnogenera that are restricted to the Proterozoic are generally uncommon and geographically restricted (Crimes, 1989).

Proterozoic–Cambrian boundary in Newfoundland

Narbonne et al. (1987; also see Landing et al., 1989) have proposed that outcrops of Member 2 of the Chapel Island Formation at Fortune Head, Newfoundland, be designated as the global stratotype of the Proterozoic–Cambrian boundary. The lower part of the formation is relatively barren of body fossils, but fossil traces are abundant throughout the formation. In a bold and innovative proposal, Narbonne et al. (1987) defined the local Proterozoic–Cambrian boundary with trace fossils. They placed the highest Proterozoic strata in a new *Harlaniella podolica* Zone that was defined by the presence of the eponymous ich-

nospecies and designated the immediately overlying Cambrian strata as the *Phycodes pedum* Zone. The base of the latter zone was defined by the lowest occurrence of *P. pedum*. Body fossils (*Sabellidites* and vendotenids) occur just below their proposed boundary and range upwards into Cambrian strata. A relatively diverse shelly fauna occurs about 550 m above the proposed boundary (Narbonne et al., 1987; Landing et al., 1989).

Narbonne et al. (1987), Landing et al. (1989), and Conway Morris (1989) proposed correlations between the Avalonian strata of Newfoundland and many of the important boundary sections located elsewhere in the world. It is evident from this preliminary work that ichnology has the potential to provide useful criteria to define the Proterozoic–Cambrian boundary and correlate that boundary between siliciclastic-dominated sections. In other regions of the world where Early Cambrian sediment accumulation was dominated by carbonates, correlations based upon ichnofossils are more problematic, because the traces are often not preserved in carbonate facies. A further concern is that the boundary and resulting correlations might differ in position from a boundary defined by skeletal fossils. These concerns notwithstanding, the central concern in extending the ichnological correlations is the stratigraphic distribution of *Harlaniella* and *Phycodes pedum*.

Harlaniella Sokolov, 1972

The stratigraphic range and biostratigraphic utility of *Harlaniella* is the subject of this report. A single species of this distinctive ichnogenus, *H. podolica* Sokolov, 1972, has been reported from Proterozoic strata from Podolia (Sokolov, 1972, 1973; Velikanov, 1990), the Kotlin Horizon on the Baltic Platform (Palij et al., 1979; Fedonkin, 1987), and Newfoundland (Bengtson and Fletcher, 1983; Crimes and Anderson, 1985; Narbonne et al., 1987). Aitken (1984) reported a trace fossil that resembles *Harlaniella* from the Mackenzie Mountains of northwest Canada. To date, there have been no reports of *Harlaniella* from Phanerozoic strata. This trace has become a critical fossil in the ongoing effort to define and correlate the Proterozoic–Cambrian boundary.

Wood Canyon Formation

The Lower Cambrian Wood Canyon Formation is a heterolithic unit that crops out throughout a broad area in the southwestern Great Basin from Death Valley, California, eastward into Nye County, Nevada. The formation was named by Nolan (1924, cited in Stewart, 1970) and subsequently subdivided into informal members (lower, middle, and upper) by Stewart (1966, 1970). The thickness of the unit is strongly variable, and it generally thins to the southeast. Diehl (1974) interpreted the formation's depositional environment as a shallow, marginal marine setting on a broad, passive continental shelf (Stewart and Suczek, 1977). More recently, Fedo and Prave (1991) have reinterpreted portions of the Wood Canyon Formation as a continental braidplain deposit. In particular, the middle member of the formation is probably a continental, not a marine, deposit.

Throughout much of its areal extent, the Wood Canyon Formation is poorly fossiliferous. However, trilobites (Diehl, 1974; Nelson, 1976; Signor and Savarese, 1988; Hunt, 1990; Mount et al., 1991), archaeocyathans (Stewart, 1970; Gangloff, 1976), "pteropods" (Diehl, 1979; probably orthothecid hyoliths), *Volborthella* (Licari and Licari, 1987), *Helicoplacus* (Signor and Savarese, 1988), and other fossils have been

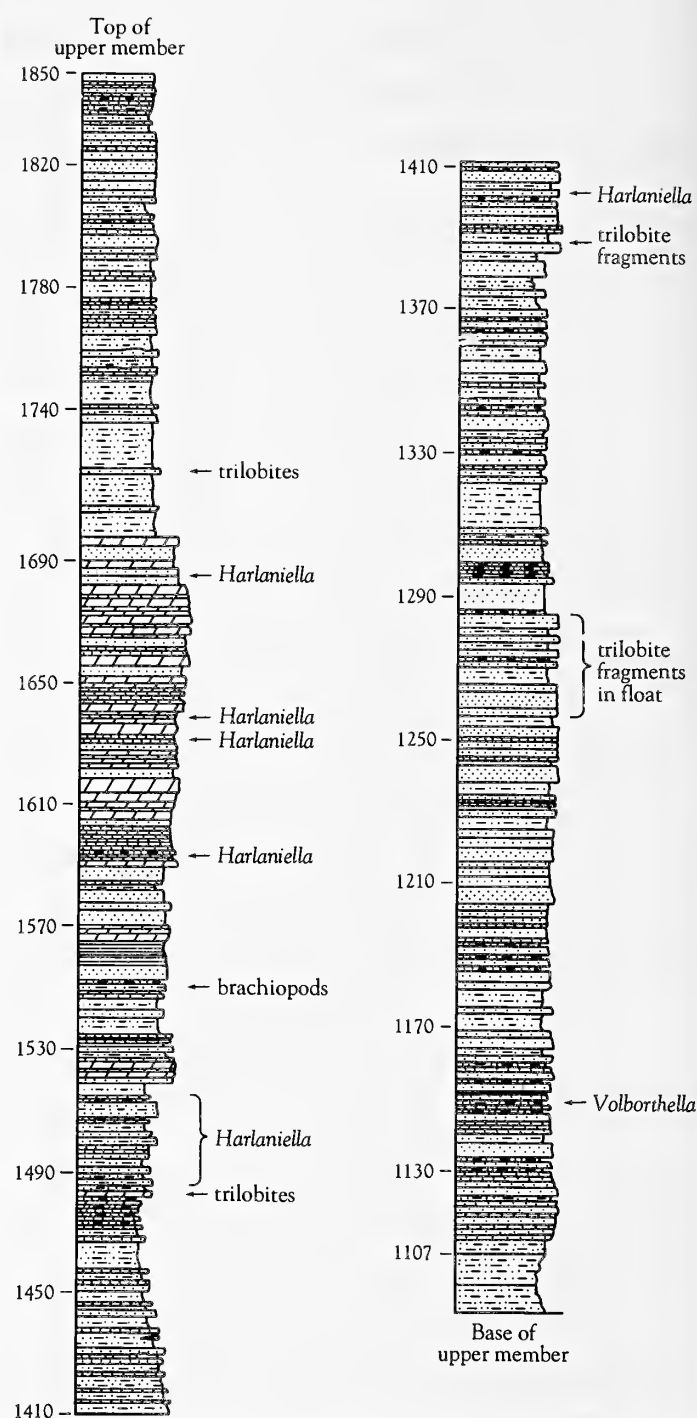


Figure 1. Upper Member, Wood Canyon Formation. Stratigraphic column for the upper member of the Wood Canyon Formation, Death Valley, California, modified from Diehl (1974). The new ichnospecies occurs within the resistant quartz sandstones of the upper member. Occurrences of *Harlaniella confusa* n. ichnosp. are indicated by an arrow.

reported from the upper member of the formation. Fossiliferous outcrops are generally limited to the northeastern exposures, especially outcrops in Eureka Valley, Titanother Canyon, and Daylight Pass. Archaeocyathan bioherms, trilobites, helicoplacoid echinoderms, orthothecid hyoliths, and other taxa are not unusual in these areas

(Signor and Savarese, 1988). These occurrences have not been described in detail, and no synoptic treatment of the fauna is available.

Lower Cambrian strata of the Death Valley region are the onshore temporal equivalents of the well-known strata of the White-Inyo Mountains (Stewart, 1970; Palmer, 1971; Nelson, 1976). Correlations between the Wood Canyon Formation and other stratigraphic units in the Great Basin are somewhat imprecise; this imprecision reflects the dearth of fossils in the lower two members of the formation and our rudimentary knowledge of the paleontology of the upper member. Stewart (1970), Nelson (1976), Signor and Mount (1989), and Mount et al. (1991) presented preliminary correlations between the Wood Canyon Formation and Lower Cambrian strata of the more northwesterly White-Inyo region. Stewart et al. (1984) offered a correlation between the Lower Cambrian of Sonora, Mexico, and the Death Valley region. Imprecise correlations notwithstanding, Stewart (1970), Nelson (1976), Signor and Mount (1989), and Mount et al. (1991) agree that the Wood Canyon Formation is entirely Cambrian in age and that the top of the formation extends into the *Bonnia*-*Olenellus* Zone. The Wood Canyon Formation correlates with the Deep Spring, Campito, and Poleta Formations and the lower part of the Harkless Formation of the White-Inyo region (Stewart, 1970; Signor and Mount, 1989; but compare Mount et al., 1991). Strata of the two regions are now juxtaposed, rather than laterally intergradational, as a result of Mesozoic and Tertiary strike-slip and thrust faulting (see Stewart, 1970). The stratigraphic paleontology of the White-Inyo region is summarized in Onken and Signor (1988).

Spiraled ichnofossils: *Harlaniella*

Diehl (1974, 1979) reported abundant spiraled traces in sandstones of the upper member of the Wood Canyon Formation. The traces are preserved as distinctive molds in resistant quartzitic sandstones. The traces are distributed throughout the outcrop area of the formation but are stratigraphically restricted to the middle and upper parts of the upper member. Consequently, they aid in the recognition of the upper member in the field.

The quartzitic sandstones of the upper member of the Wood Canyon Formation tend to be white to tan, medium- to massively bedded, resistant units. The traces are preserved as concave endichnia within these sandstones. The original filling of the burrows is unknown, but it was probably calcareous material that was subsequently leached from the sandstone. The traces tend to parallel bedding surfaces but curve and bend in all directions through the rock. Where they occur, the traces are abundant and readily apparent on fractured surfaces.

These sandstones with spiraled traces are interbedded with trilobite-bearing shales in Titanother Canyon and at Daylight Pass, within Death Valley National Monument. The shales contain *Fallotaspis* (Hunt, 1990; Mount et al., 1991), nevadiid and nevadellid trilobites (Stewart, 1970), and, higher in the section, *Olenellus* and *Wanneria* (Mount et al., 1991; P.W. Signor, personal observation). These trilobites define the age of the upper portions of the upper member of the Wood Canyon Formation as middle to late Early Cambrian (*Fallotaspis*, *Nevadella*, and *Bonnia*-*Olenellus* Zones).

Diehl (1974, 1979) was apparently unaware of Sokolov's genus *Harlaniella*, which was described in 1972. The small, spiraled burrows are distinctive and not easily confused with other ichnogenera. Diehl did not offer a binomial name or formal description of his spiral traces, although he did employ them to identify the upper member of the Wood

Canyon Formation in the field. Comparison with material from the Baltic Platform and the Chapel Island Formation in Newfoundland indicates the Wood Canyon spiral molds are *Harlaniella*, although sufficient differences exist to warrant erection of a new ichnospecies.

Discussion

The new species reported herein extends the range of Sokolov's ichnogenus, *Harlaniella*, into the Phanerozoic. The utility of *Harlaniella* as an index ichnofossil for the late Proterozoic (e.g., Bengtson and Fletcher, 1983; Crimes, 1989; Velikanov, 1990) is thereby diminished. Nevertheless, the range of the ichnogenotype, *Harlaniella podolica*, remains restricted to the Proterozoic. The range of variation of Sokolov's ichnospecies is not well-defined, and further research might indicate that *H. confusa* n. ichnosp. falls within the range of variation of *H. podolica*. In any event, the rocks of the basal portion of Member 2 of the Chapel Island Formation also contain the trace *Palaeopascichnus delicatus*, which is restricted to the Proterozoic (Narbonne et al., 1987). Thus the results presented here cast no doubts upon the age of the Chapel Island Formation.

Systematic ichnology

Ichnogenus HARLANIELLA Sokolov, 1972

Discussion.—Sokolov's original diagnosis and subsequent descriptions of the ichnogenus are sketchy, but no refinement will be attempted herein because neither the original material nor additional material from Podolia or the Baltic region are available. The diameters of the fossil traces vary from 1 to 4 mm (Palij et al., 1979; Sokolov [1973] reported diameters of 3 to 4 mm). The groove incised into the trace spirals at an angle of 45° to 80° from the axis of the tube. The distance along the trace between successive passes of the spiral line varies from 0.5 to 0.8 mm (Sokolov, 1973; Palij et al., 1979). The orientation of the traces relative to the bedding surfaces is not recorded, although the illustrations suggest that the traces generally parallel bedding. The original description makes no mention of the presence of branching, but Sokolov's (1973, Fig. 3.4) illustration of the holotype clearly shows a bifurcating trace. Sokolov's 1973 illustration of his holotype does not appear to match Palij et al.'s (1979) illustration of the holotype.

Geologic range.—Late Vendian (Kotlin Horizon of the Valday Series) to late Early Cambrian (lower *Bonnia*-*Olenellus* Zone, probably equivalent to the lower Toyonian Stage).

HARLANIELLA CONFUSA n. ichnosp.

Figure 2A-E

Diagnosis.—Small cylindrical traces with a groove irregularly spiraled obliquely to the axis of the trace; coiling direction and angle of spiral locally reverse direction; traces are subparallel to bedding and irregularly curved in an apparently random pattern.

Description.—Small, unbranched traces with a circular cross-section and a spiraled groove oriented obliquely to the burrow. The angle of the spiraled groove to the axis of the tube is highly variable, ranging from 0° to 40° in either direction. The diameters of the traces vary from 1.5 to 2.5 mm. The distance along the axis of the trace between successive spiral grooves varies from 1.0 to 1.4 mm. Traces are generally oriented parallel to bedding surfaces but are not restricted to a single bedding-plane. Branching has not been observed.

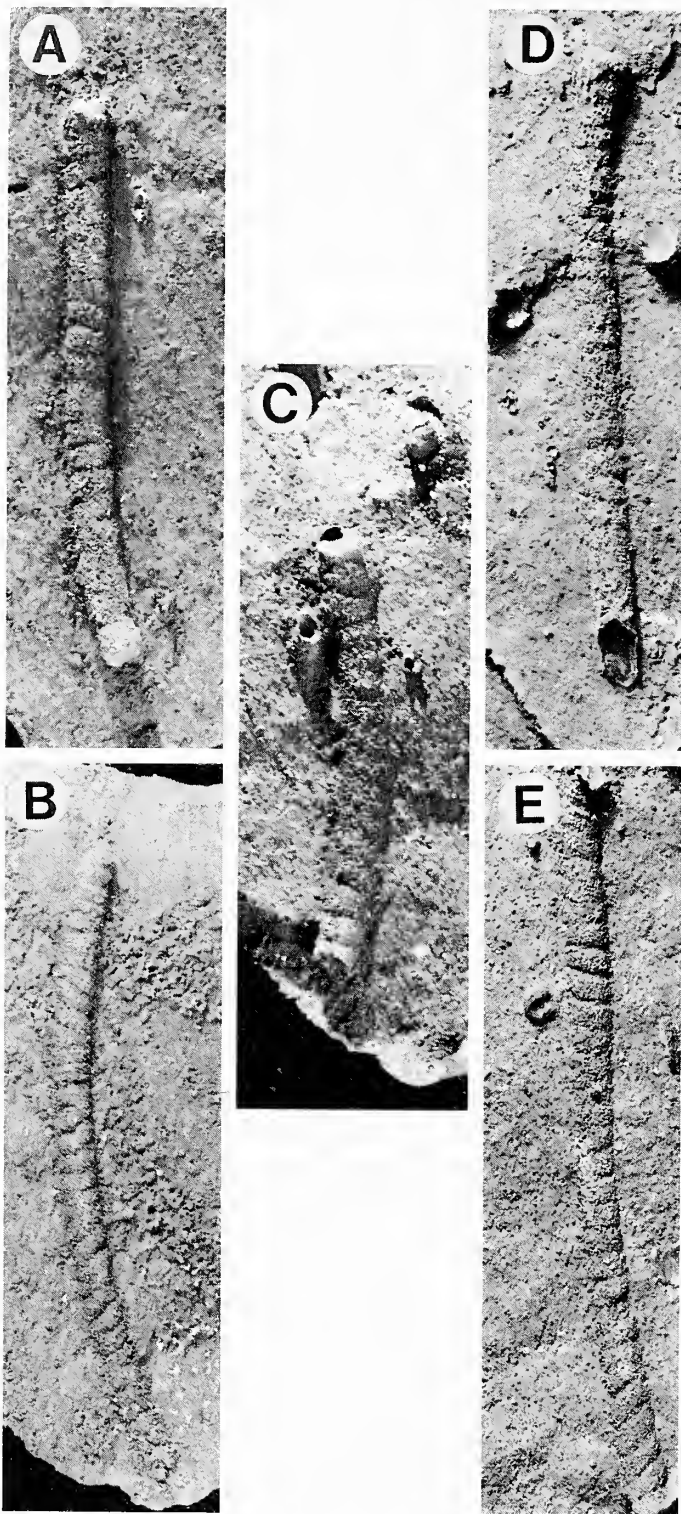


Figure 2. *Harlaniella confusa* n. ichnosp. All illustrated specimens are from the upper member of the Lower Cambrian Wood Canyon Formation. A, Paratype, UCMP 38664, x2.3. B, Paratype, UCMP 38665, x1.8. C, Paratype, UCMP 38666, x2.6. D, Paratype, UCMP 38666, x2.5. E, Holotype, UCMP 38663, x1.9. The curious reversal of the spiraling that characterizes this new ichnospecies can be seen in B and E. All specimens illustrated herein are latex casts of concave endichnia that have been whitened with ammonium chloride for photography.

Discussion.—*Harlaniella confusa* n. ichnosp. is preserved as molds (concave endichnia) in resistant sandstones of the upper member of the Wood Canyon Formation. The original filling of the burrows is unknown. The molds are rarely preserved on bedding surfaces, but short segments are commonly found on fractured surfaces within beds. The “spiral traces” are a useful field mark for the upper member of the formation (Diehl, 1974, 1979).

Harlaniella confusa n. ichnosp. differs from *H. podolica* in the density of the spiral grooves, the occasional reversals in the direction of the spiral, and the apparently random orientation of the spiral traces within the rock. The direction of the spirals in *H. confusa* n. ichnosp. are predominately dextral (with the axis oriented vertically, the groove appears to move from lower left to upper right), as in *H. podolica*, but the groove occasionally spirals sinistrally (Figure 2B, E). In addition, *H. podolica* has a higher density, or closer spacing, of the grooves. The distance between successive grooves in *H. confusa* n. ichnosp. is 50% greater than reported for *H. podolica*.

There is a direct geometric relationship between the angle of the spiral groove and the tube axis (for geometric simplicity, the complement of this angle is employed as Θ : Θ is the angle between the spiral line and a line perpendicular to the axis of the trace), the diameter of the tube ($2r$), and the distance between successive grooves on the surface of the tube (h). This value is given by the relationship:

$$h = 2\pi r [\tan(\Theta)] \quad (1)$$

In essence, the distance between successive grooves increases with an increase in Θ . The remarkably consistent distance between grooves on one side of the traces (see Figure 2) strongly suggests that the angle of the groove compensates for large angles on one side of the trace with corresponding small angles on the other, hidden side. Intuitively, this is the only way that the apparently transverse lines seen in some specimens (e.g., Figure 2D, center) can be formed by a spiraled line. In other words, the pattern of spiraling on different sides of the tube is not a simple mirror image.

Harlaniella confusa n. ichnosp. appears to represent the trace of small burrowing organisms that moved within the sediment. The traces show no evidence of systematic mining of the sediment, as seen in many traces left by deposit feeders. The trophic role of the trace-maker is problematical, given the limited data at hand, but it seems likely to have been the trace of a predatory, bilaterally symmetrical metazoan.

Type locality.—Titanother Canyon in Death Valley National Monument is the type locality for the new ichnospecies (UCMP M-7293: unsurveyed area west of section 19, T13S R46E, Grapevine Peak 15-minute Quadrangle, 1957 edition). This is probably at or near Stewart's (1970) locality number 8. Additional material was collected from Titanother Canyon (UCMP M-7292: section 30 T13S R46E, Grapevine Peak 15-minute Quadrangle, 1957 edition); Echo Canyon, Death Valley National Monument, California (UCMP M-7294: unsurveyed, sec. 11, T27N, R3E, Ryan 15-minute Quadrangle, 1952 edition); and Emigrant Pass, east of Tecopa, CA (UCMP M-7295, Section 25, R8E T21N).

Geologic range.—Middle Lower Cambrian (*Fallotaspis* Zone to lower *Bonnia*–*Olenellus* Zone).

Material.—Seven blocks of quartzitic sandstone with abundant fossil traces preserved as concave endichnia, repositied at the University of California Museum of Paleontology. The specimen numbers are holotype, UCMP 38663; paratypes 38664–38667.

Acknowledgments

G.M. Narbonne and E. Landing reviewed an earlier draft of this manuscript and made many useful improvements. I thank G.M. Narbonne for discussions and access to specimens. T.P. Crimes examined and commented upon the Death Valley material. G.J. Vermeij discussed spirals with me. Thanks are also given to the Supervisor of Death Valley National Monument for permission to collect within the boundaries of the Monument. This research was supported by NSF EAR 88-04798. PWS supplied \$250 toward publication of this report from his faculty research grant.

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Hexagonaria and the Hexagonariinae (Disphyllidae, Rugosa): Devonian colonial corals

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Abstract

Definition of the Family Disphyllidae has suffered from confusion regarding several of its important genera; one is the genus *Hexagonaria* (emend.) with its type species, *H. hexagona*. The latter has yardarm-like carinae that have overly influenced the diagnosis of the genus. *Hexagonaria* as a genus should be broad enough to include both colonies with heavily dilated septa and yardarm-like carinae, and those at the other end of the spectrum with only slightly dilated septa and/or without visible carination. *Hexagonaria bassleri* and *H. oweni* from the Frasnian of Iowa clearly show the range of variation that can be expected within species of this genus. This variation is sufficient to include both the genera *Pseudohexagonaria* Kramer, 1982, and *Argutastrea* Crickmay, 1960, as originally defined, but need not include either genus as revised by Coen-Aubert and Lutte (1990). Non-carinate cerioid corals should not be placed in the genus *Disphyllum*. The Subfamily Hexagonariinae, as defined by Hill (1981), includes the "closely carinate" cerioid genera *Hexagonaria* and *Haplothecia*, as well as the poorly known genus *Marisastrum*. This subfamily grouping is abandoned herein because the former two genera cannot belong together. *Hexagonaria* has broad monacanthine septal trabeculae that form sporadic yardarm-like carinae as part of an ontogenetic process that led to septal dilation. *Haplothecia* has narrow monacanthis and true yardarm carinae in attenuate septa. *Haplothecia* is closely related to *Frechastrea*; the two genera belong in the Phillipsastreidae, and perhaps in their own subfamily.

Introduction

The Family Disphyllidae Hill, 1981, is a group of widespread Devonian fossil corals. These corals, along with the Family Phillipsastreidae, are among the most common and typical of Middle and Upper Devonian rugosans and occur in major outcrop areas throughout the world. As work has progressed on the description and understanding of Devonian rugose coral faunas, a multiplicity of names, and taxonomic confusion, have resulted from imperfect interpretations of taxa and generic morphology. Varying diagnoses of the genus *Hexagonaria* have resulted in confusion about some colonial genera of the Disphyllidae and how to subdivide the family into subfamilies.

In the study of rugose corals, the taxonomic significance of morphologic features, the relative importance of these features, and the level of

variation to be expected within taxa from different faunal provinces and/or different ecologic settings frequently cause problems. Major difficulties also arise from an overly typological approach to individual coral genera and species. This typological approach develops from the failure to evaluate populations of fossil species, especially with respect to morphologic variation. Further confusion results from variable terminology. Different authors use terms for morphologic characters, such as carinae, monacanthine trabeculae, and trabecular fans, to refer to different features. Many reports have also caused confusion because they do not utilize standard definitions (see Hill, 1981, pp. 332-336, for glossary). In the interpretation of the Devonian rugose coral Family Disphyllidae, variable usage of these terms has resulted in varying interpretations of species and genera. A case in point is the definition and usage of the genus *Hexagonaria*, its component species, and the makeup of subfamilies within the Disphyllidae. This report focuses on the definition of *Hexagonaria* and its type species *H. hexagona*, the characteristics used to define the genus and species, their utility, and their effect on the definition of other genera within the Family Disphyllidae (as defined by Hill, 1981). This report does not reevaluate the validity and morphology of all genera of the Disphyllidae.

As part of a restudy of the Upper Devonian (Frasnian) rugosan fauna of north-central Iowa, several species with great similarity to *Hexagonaria hexagona* have been examined in population samples of twenty-five to fifty colonies. The species *Hexagonaria bassleri* (Webster and Fenton, in Fenton and Fenton, 1924) in particular shows many of the characteristics that have been utilized by various authors to define species or even genera of disphylliid corals. These features vary greatly within this single species in a population sample of reasonable size.

The species *Hexagonaria hexagona*

Lang and Smith (1935, p. 550) chose *Cyathophyllum hexagonum* Goldfuss, 1826, p. 61, as the genotype species of the genus *Hexagoniophyllum* Gurich, which they regarded as a synonym of *Prismatophyllum* Simpson. *Hexagoniophyllum* Gurich, 1909, was later placed into synonymy with *Hexagonaria* Gurich, 1896, by Lang et al. (1940, p. 69). Lang and Smith (1935, p. 550) also selected a lectotype for the species from the Goldfuss collection at the University of Bonn; this specimen had been illustrated by Goldfuss (1826, Pl. 20, fig. 1a, 1b).

The first modern description of *Hexagonaria hexagona* was by

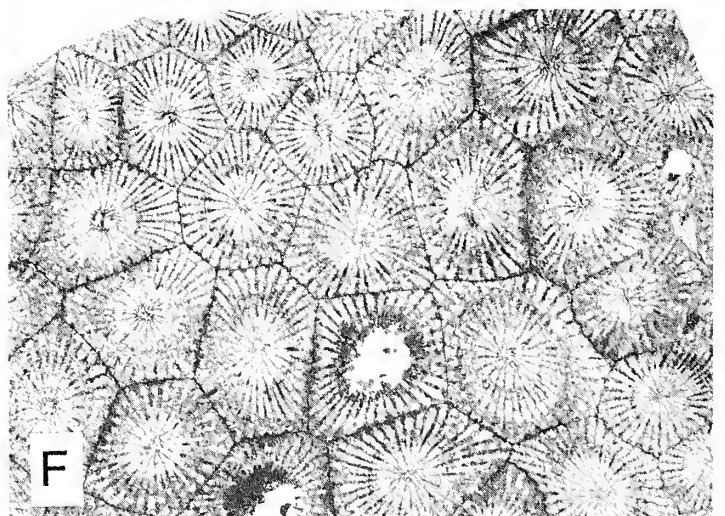
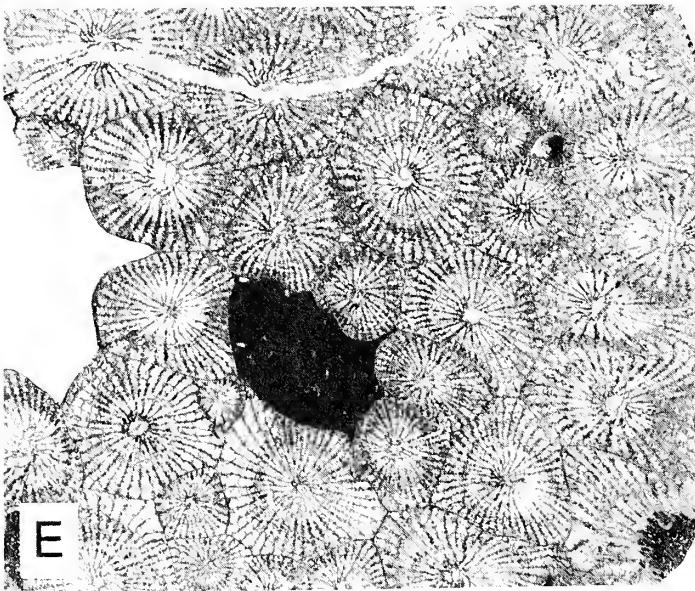
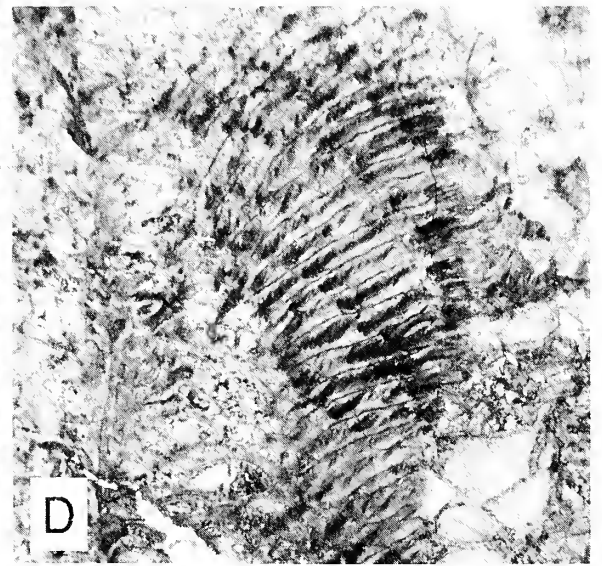
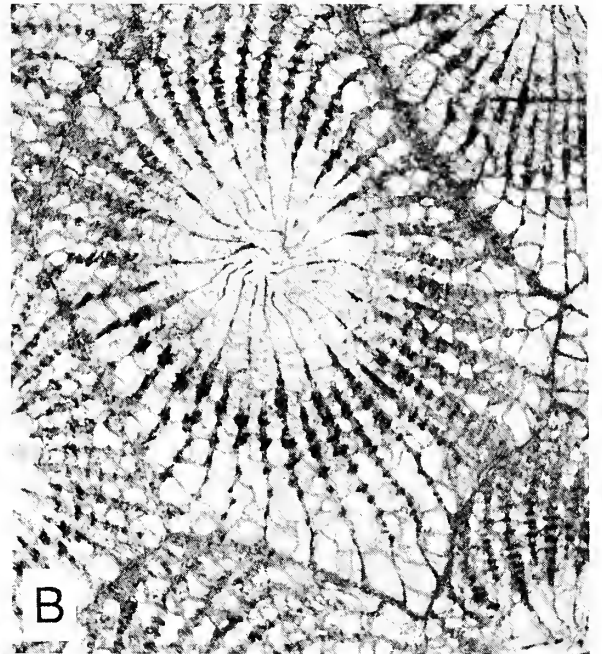
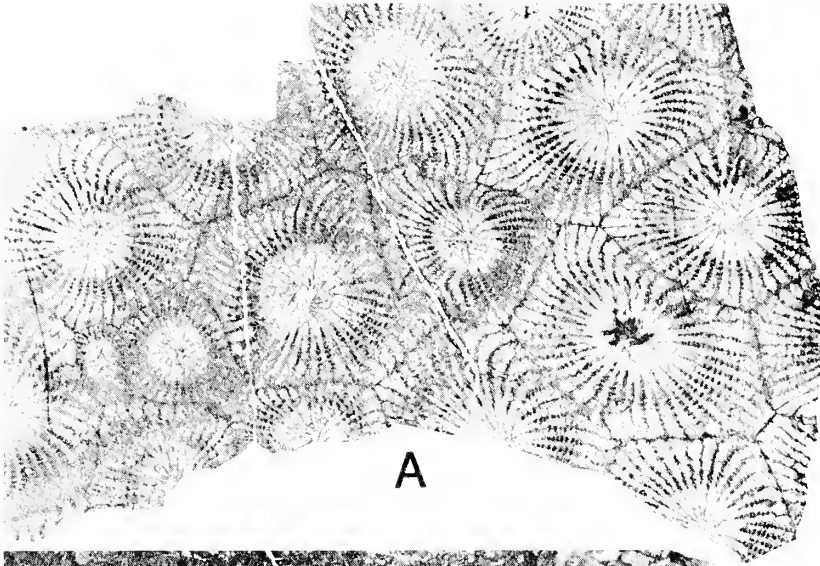


Plate 1. *Hexagonaria* spp. *A-D*, *Hexagonaria hexagona*, topotype from Refrath Beds in "Steinbreche," near Refrath, Germany, USNM 455876. *A*, Overview of transverse section, x2; *B*, Enlarged corallites illustrating variability in the formation of septal carination, x5; *C*, Longitudinal section of corallite to show configuration of septal trabeculae and dissepimentarium, x6; *D*, Enlarged view of lath-like septal trabeculae with feathery structure within monacanth, x10; *E, F*, *Hexagonaria bassleri*, Lime Creek Formation, north-central Iowa, to illustrate variation in septal weight and ornamentation, both x2; *E*, Colony (SUI 64791) with heavy septal dilation and sporadic carination (arrow); *F*, Colony (SUI 64792) with less septal dilation.

Stumm (1948), who published a description of thin sections of a toptype from Bensberg, Germany (University of Michigan Museum of Paleontology 23660). He stated that he described it because the species' "internal structure has never been illustrated" (Stumm, 1948, p. 14). He noted that "Both orders of septa are carinate, with yardarm carinae predominating. In some corallites carinae are not present on all the septa, and in others they may be present only on the parts near the margins of the tabularia" (Stumm, 1948, p. 14). Stumm's (1948, Pl. 6, figs. 1, 2) thin-section photographs show the type of carination seen in other toptype specimens of the species. They are broad, yardarm-like carinae that are strongly developed as a result of the process of septal dilation. Some septa of the corallites are more carinate than other septa within the same individual. His longitudinal section shows trabeculae that bend inward as the dissepiments become more steeply inclined axially near the outer boundary of the tabularium. It is noteworthy that the specimen of *H. hexagona* illustrated by Stumm (1948) possesses large corallites, but their tabularia are approximately the same diameter as North American species shown on the same page. A major part of the large corallite diameter is due to a very broad dissepimentarium in this *H. hexagona* specimen.

Flügel and Shimunek (1960, p. 5, Pl. 1, fig. 1) examined and illustrated a Goldfuss specimen that they regarded as the lectotype chosen by Lang and Smith for *H. hexagona*. However, they stated that it could not have been the specimen illustrated by Goldfuss (1826, Pl. 20, fig. 1a, 1b), but rather that it was the individual shown in Pl. 20, fig. 1a. This specimen was formally chosen by them as the lectotype for the species. They noted that the species is characterized by septal dilation and that septa can bear yardarm-type carinae in the dissepimentarium (Flügel and Shimunek, 1960, p. 5). These authors also briefly described a possible toptype, which they stated came from Paffrath, Germany (UGP 760, University of Graz). Paffrath is on the east side of Cologne, approximately 5 to 6 km north of Refrath, the type locality of the species. The locality for the Graz specimen is probably simply misidentified.

Pickett (1967, p. 59) argued convincingly that the specimen chosen as the lectotype by Flügel and Shimunek (1960) was not a specimen figured by Goldfuss (1826), but that it was the only specimen in the Goldfuss collection in Bonn which, in fact, belonged to either the genus or the species. This also meant that the specimen selected as the lectotype by Lang and Smith (1935) was not in the collection. He thus chose as the neotype for the species the specimen figured by Flügel and Shimunek (1960), which is specimen GMB0 207c in the Goldfuss collection in the Geological Museum at the University of Bonn. This concept of the neotype has been accepted by all subsequent workers. In his description of the neotype, Pickett (1967, p. 60) noted quite rightly that "Im ausseren D:arium können alle Septen...Carinae tragen." That translates to say that all septa can bear carinae in the outer dissepimentarium, but obviously does not state that all septa bear carinae. Pickett's (1967, Pl. 4, fig. 15) photo of the neotype shows that the occurrence of carinae is not uniform throughout this transverse section. Many of the septa in illustrated corallites do not have obvious yardarm carinae, and none have uniformly distributed carinae. In none of the illustrated corallites are all septa carinate, and yardarm carinae are uniformly distributed on one or two septa only.

Birenheide (1969, p. 40) discussed and figured the neotype chosen by Pickett (1967), but did not redescribe it. On the following page, he placed *Prismatophyllum*, with numerous yardarm carinae and undilated septa, in synonymy with *Hexagonaria*. He noted that the type locality should be regarded as the "Steinbreche" near Refrath, which later was the source of toptype material described by Kramer (1982) and now in

this report. Birenheide (1969, p. 40) also emphasized the Frasnian age of the Refrath Beds exposed at the "Steinbreche."

Kramer (1982) also briefly described one toptype from the Refrath Steinbreche and illustrated thin sections of the specimen (GIK 939, University of Cologne). An additional toptype specimen was collected by the author in the fall of 1969 from the Refrath Steinbreche (No. 455876, U.S. National Museum), and thin sections are illustrated on Plate 1 of this paper. Like all other material from the locality, this specimen of *Hexagonaria hexagona* has large corallites with heavily dilated septa. The prominent dilation of the septa is striking, as is the presence of stout, yardarm-like carinae in many corallites in the colony.

A description of the species, based on the neotype and the three toptypes noted above, is as follows:

HEXAGONARIA HEXAGONA (Goldfuss, 1826)

Plate 1, figures A-D

Description.—Flattened hemispherical coralla with large, six-sided corallites characterized by flat calicinal platforms and steep-walled calicinal pits.

The corallites are large; mature-appearing individuals in the toptype (No. 455876 USNM) have tabularia with diameters ranging from 5.65 to 7.3 mm (mean of 6.55 mm for six corallites). The corallite diameters range from 10.5 to 17.5 mm (mean of 13.7 mm); corallites bear from forty to forty-two septa divided equally into major and minor orders (mean of 40.7). Pickett (1967, p. 60) noted that the neotype has forty-two septa in mature corallites and calices up to 20 mm in diameter, although seldom more than 17 mm. The University of Michigan toptype has corallites that are 15 to 22 mm in diameter, with tabularia averaging 5 mm in diameter and thirty-four to forty-two septa in mature corallites (Stumm, 1948, p. 14). The University of Cologne toptype has somewhat smaller corallites (13-14 mm) than the Bonn neotype or the USNM toptype, and fewer septa (thirty-four to thirty-six) according to Kramer (1982, p. 661).

In transverse view, the septa clearly are differentiated into major septa that extend nearly to the axis of the corallites and minor septa that reach only a short distance into the tabularium. All septa are greatly dilated in the inner dissepimentarium; the neotype and toptypes all greatly resemble each other in their septal dilation (Plate 1, figure A). The greatest dilation is in the innermost dissepimentarium, and both major and minor septa rapidly thin as they extend into the tabularium. The dilated portion of the septa is almost spear-shaped, although this shape is generally described as spindle-shaped, especially in European reports. The septal trabeculae reach their greatest width in the area of maximum dilation, and some septa may have trabecular ridges on septal flanks in this area. Usually the lateral expansion of trabeculae can be accommodated within the dilated septa. As septa extend towards the periphery of the corallites, the dilated septa of the inner dissepimentarium become more attenuate (Plate 1, figure B). Where heavy septa are developed, the lateral expansion of trabeculae continues, so that there is the appearance of yardarm carinae. Corallites with thin septa may have strongly developed yardarm-like carinae in the inner dissepimentarium and small, knobby, expanded trabeculae in the outer dissepimentarium. At the extreme, septa are smooth and thin, without visible trabeculae. All septa can have some form of "carination," but not all septa within one colony have them.

Intercorallite walls are typical of cerioid colonies, and the walls are straight in the neotype and toptypes, with the epithecal path appearing straight or wavy in transverse section. The walls, where thick, have massive pyramidal bases of the septa incorporated into the wall struc-

ture (Plate 1, figure A); where thin, the walls have thin septa that abut them perpendicularly.

In longitudinal section, *Hexagonaria hexagona* has a wide dissepimentarium of five to ten globose dissepiments in each row. The dissepiments are larger and slightly flattened in the peripheral part of the dissepimentarium, whereas in the inner portion dissepiments are always somewhat ovate and steeply inclined adaxially.

As is usual for members of the family with long septa, *Hexagonaria hexagona* has an axial row of cap-shaped, flat-topped tabulae and periaxial rows of trough-shaped tabulae. This feature is imperfectly developed in the USNM topotype (Plate 1, figure C), but was noted by Pickett (1967, p. 60) in the Bonn neotype and was illustrated by Kramer (1982, p. 662) in the Cologne topotype specimen.

The septal trabeculae are the lath-like monacanthi typical in the Disphyllidae, and have a sharp line of junction (or abutting) between neighboring trabeculae (Plate 1, figure D). The monacanthi may be clear laths or, where thickened, tend to be dark in the center and show a feathery internal structure. The monacanthi form a variable angle with the corallite wall and bend progressively inward to remain perpendicular to the rows of dissepiments (Plate 1, figures C, D). Thus there is a progressive bending or angular inclination towards the outer border of the tabularium. This has been referred to as a "half-fan," but the term should not be used, because it incorrectly implies homology to the trabecular fans of septa in the Phillipsastreidae.

Remarks.—This is a typological description of *Hexagonaria hexagona*, based on a neotype and three topotype specimens from Steinbreche near Refrath. The Bonn neotype and the USNM topotype are remarkably similar in the appearance of corallites, septa, and septal ornamentation. The Cologne topotype closely resembles the other two but apparently has fewer septa, whereas the Michigan topotype, as illustrated, may have less-pronounced septal dilation and ornamentation. It is improbable that the species existed only in this one area (which was quarried). Thus it is suggested that the neotype and topotypes are eco-variants of what would have been a more broadly distributed species. If this is true, other variants of the same species should be identifiable in Frasnian strata of northwestern Europe.

The genus *Hexagonaria*

Devonian species of the genus *Hexagonaria* have been variably described by many authors. Space is not available here to review all of these; this report focuses on standard and recent work in order to illustrate the variation in definition of the genus.

Stumm (1948, p. 12) placed cerioid colonial species with well-differentiated major and minor septa, a marginal calicinal platform, and a central calicinal pit in the genus. Regarding septal ornamentation, Stumm (1948, p. 12) noted, "Septal carinae present to some extent in most species, weakly or strongly developed. Yardarm type of carinae predominate in some species, the alternating type is more common in others." He regarded carinae as almost any type of morphologically expanded trabeculae.

Hill (1956, p. 280) described *Hexagonaria* as cerioid, with "septal thin, carinate or dilated." This is taken to mean that she included species with well-developed yardarm-like carinae, as well as species with little or no development or carination and/or development of marked dilation. At the time that this edition of the *Treatise on Invertebrate Paleontology* was written, *Hexagonaria* was still placed in a broadly defined Family Phillipsastreidae, which included most

genera that have since been placed in either the Disphyllidae or the Phillipsastreidae.

Pickett (1967), in a treatise on the Phillipsastreidae (s.l.), not only described *Hexagonaria* but also made a major contribution by clarifying the status of the type species *H. hexagona* and its neotype. Pickett also presented a diagram with the proposed evolutionary development of *Hexagonaria* from *Disphyllum*, and thus suggested that both genera might include species with or without carinate septa.

Birenheide (1978, p. 78), in his monograph on Devonian rugosans of Germany, placed *Hexagonaria* and allied genera in the Family Cyathophyllidae and Subfamily Columnariinae, and made several nomenclatural choices that generally have not been followed. In one of these, Birenheide included both cerioid and phacelloid species in *Disphyllum*, a genus he characterized as lacking septal carinae. He noted (Birenheide, 1978, p. 90), "The cerioid species of *Disphyllum* were frequently placed in *Hexagonaria*, because the characteristics of the type species of this genus were for a long time insufficiently [well] known" [author's translation]. In his description of *Hexagonaria*, he noted that "Septa [are made] out of large trabeculae, which above all in the dissepimentarium can be distributed [as] strong yardarm carinae, and peripherally are not always bound to one another" (Birenheide, 1978, p. 95). In remarking that *Hexagonaria* had been incompletely understood, Birenheide (1978) ignored the description and illustration of a topotype by Stumm (1948, p. 14). It was most certainly understood that *H. hexagona* contains yardarm carinae-like trabecular structures. The genus was, however, treated as having variably developed septal ornamentation, septal dilation, and trabeculae dilation. It is still a valid opinion that the genus should not be so narrowly defined as to require yardarm carinae, because the neotype of *H. hexagona* only has such carinae sometimes. A variable definition of yardarm carinae can likewise add confusion.

In the revision of the Rugosa for the *Treatise on Invertebrate Paleontology*, Hill (1981, p. 275) accepted Pickett's (1967) choice of a neotype for *H. hexagona* and characterized the genus as a cerioid form with fusiform septa dilated in the innermost dissepimentarium with "typically closely carinate septa with predominantly yardarm carinae...[and with]...monacanthine septal trabeculae arranged in board symmetrical fan or half-fan." Although she did not clearly exclude species without "predominantly yardarm carinae" from the genus, Hill (1981) defined the Subfamily Hexagonariinae to include only carinate corals, as discussed below.

Prior to proposal of an emended diagnosis for the genus *Hexagonaria*, a review is presented that lists key characters of the genus as they occur and vary in *Hexagonaria bassleri* from the Frasnian of Iowa. This sample consists of twenty-four colonies of the species collected from two adjacent areas in northern Iowa; these specimens are from the same horizon in the Owen Member of the Lime Creek Formation (Frasnian age).

Within the Family Disphyllidae and, in particular, within the genera *Hexagonaria*, *Disphyllum*, and other colonial forms central to the family, the following characteristics are generally regarded to be of critical importance to their taxonomy:

1. Colonial form.
2. Development of well-differentiated dissepimentarium and tabularium reflecting the calicinal configuration, with a central pit and peripheral platforms and the topography of these features.
3. Type of septal trabeculae; relationship of trabeculae to rows of dissepiments in the peripheral portions of the corallites and the configuration of trabecular patterns seen in longitudinal section.

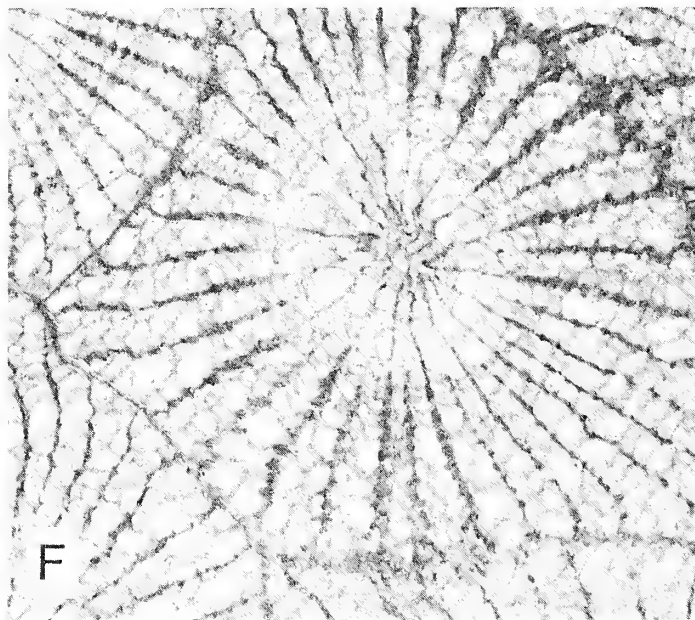
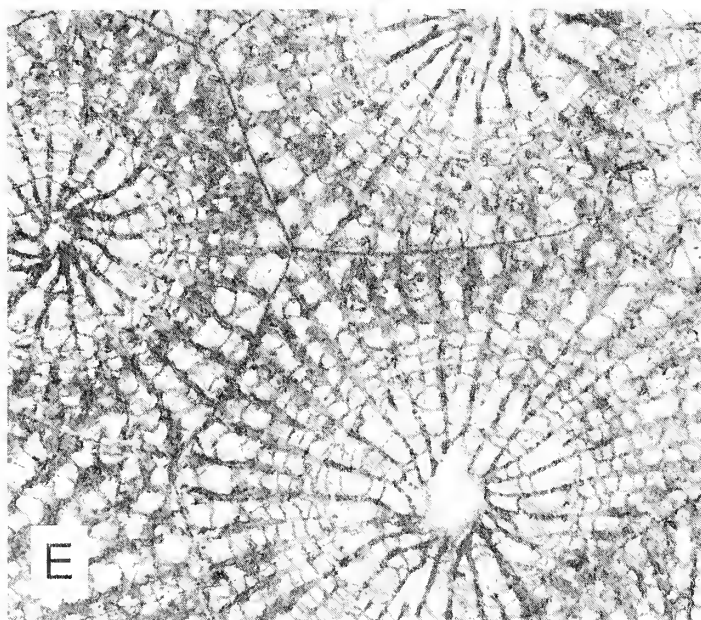
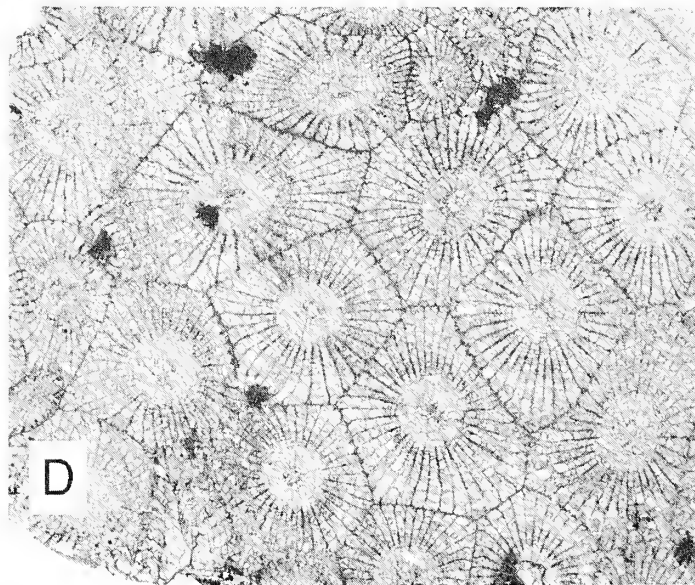
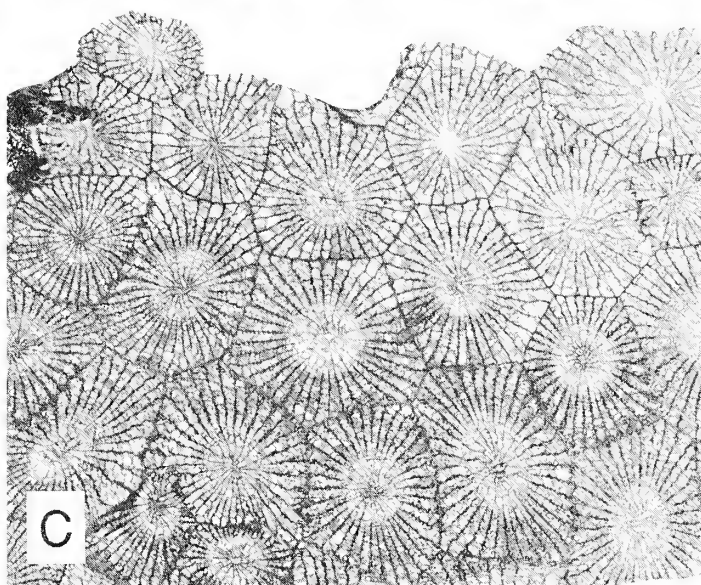
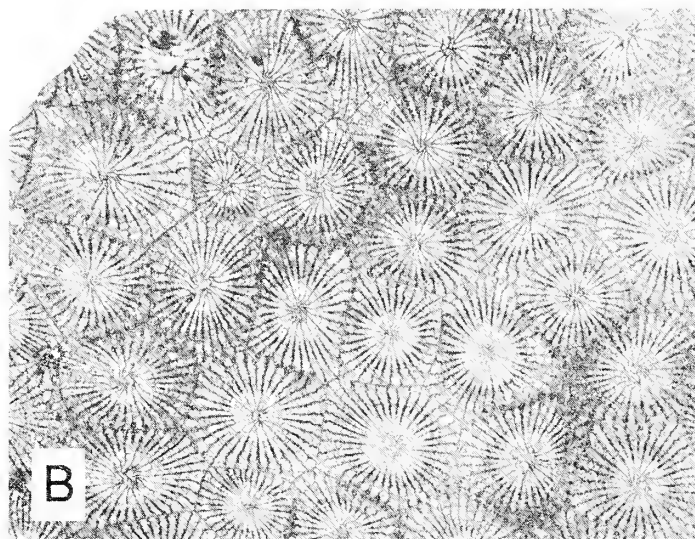
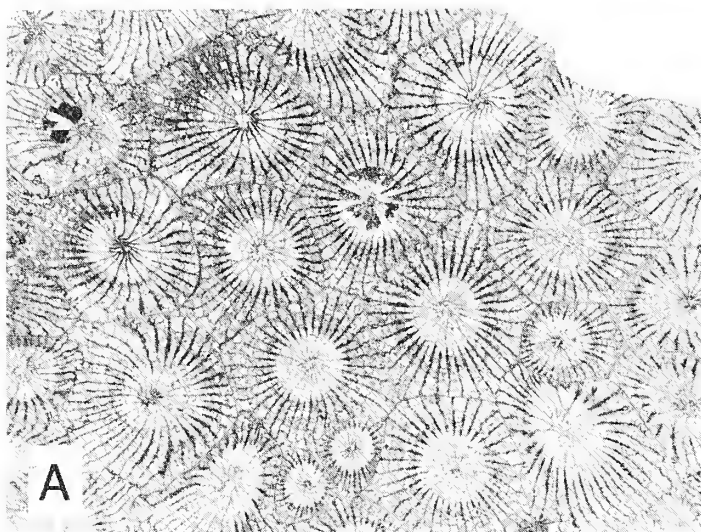


Plate 2. *Hexagonaria bassleri*, Owen Member of Lime Creek Formation, north-central Iowa. *A-D*, To illustrate variation in septal weight and ornamentation, all x2. *A*, Colony with relatively heavy dilation only in inner dissepimentarium (SUI 64793); *B*, Colony showing less dilation but sporadic occurrence of weak carination (SUI 64794); *C*, Colony with little or no septal dilation, but sporadic weak carination (SUI 64795); *D*, Colony with very little septal dilation and virtually no carination (SUI 64796). *E*, Enlargement of portion of SUI 64791, showing heavily dilated septa with no carination in outer dissepimentarium, x8. *F*, Enlarged view of SUI 64795 with variable development of septal dilation and carination, x8.

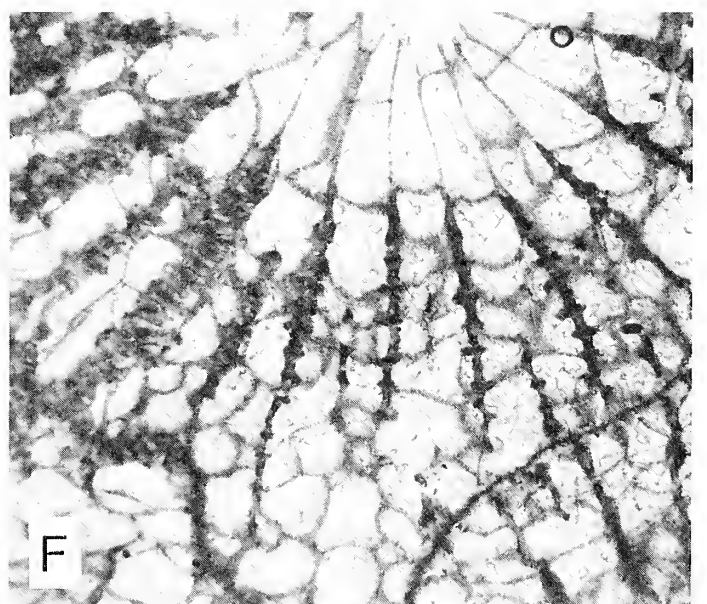
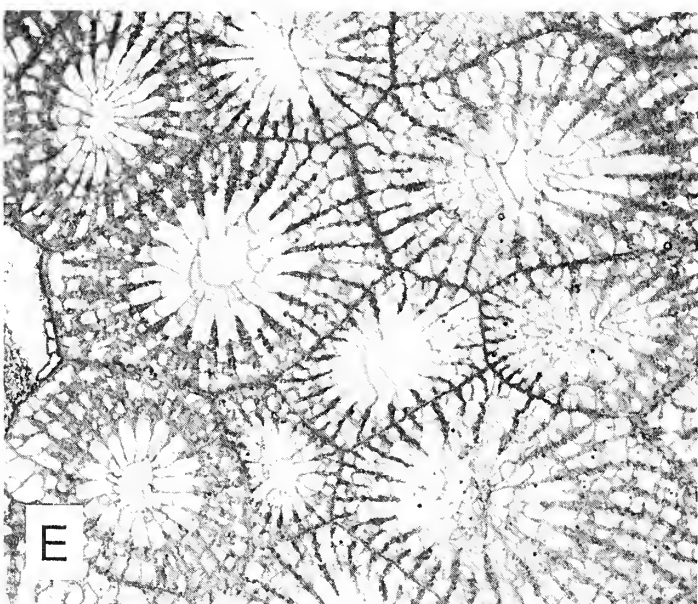
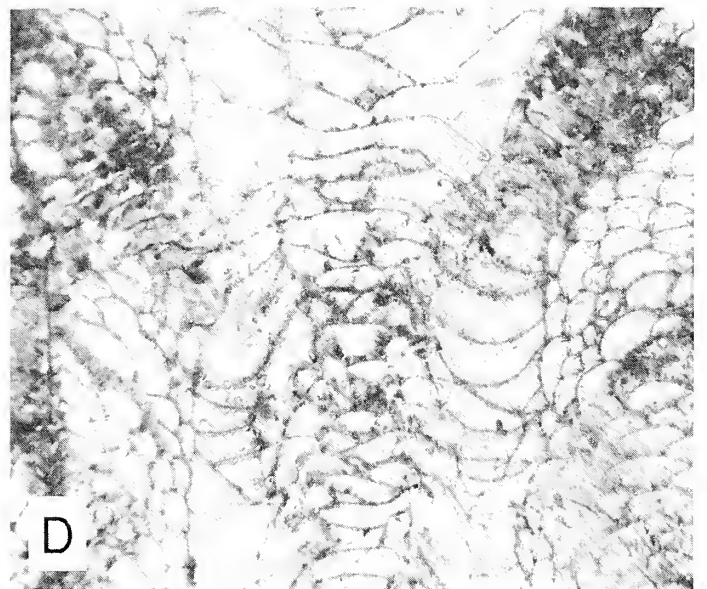
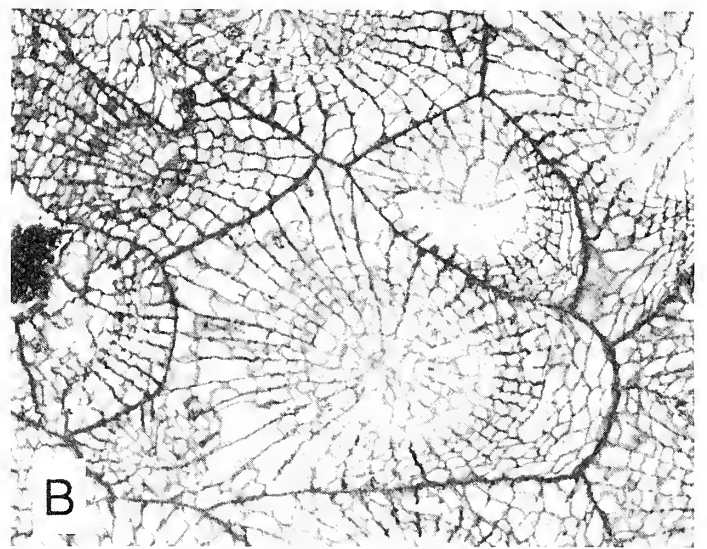
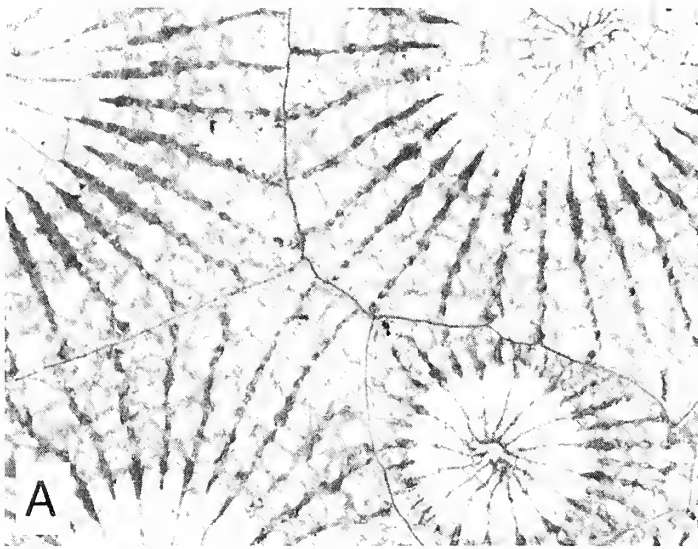


Plate 3. *Hexagonaria* spp. from north-central Iowa. *A-D*, *Hexagonaria bassleri* from Owen Member, Lime Creek Formation. *A*, Colony illustrating development of “knobby carinae” in septa (SUI 64793), x8; *B*, Colony with weak dilation of septa and development of lonsdaleoid dissepimentarium, at least in part connected with the budding process (SUI 64797), x5; *C*, Longitudinal section of corallite with variable development of uniformly inclined straight trabeculae (left side) and increasingly inclined and axially bent trabeculae (right side) (SUI 64798), x10; *D*, Longitudinal section of corallite showing variable development of dissepimentarium and axial and periaxial series of tabulae (SUI 64799), x10. *E, F*, *Hexagonaria oweni*. Shell Rock Formation, showing septal dilation and carination (SUI 64800). *E*, Overview in transverse section illustrating heavy septal dilation and triangular outline of heavy septal bases, x5; *F*, Enlarged view of portion of single corallite showing yardarm-like carinae and their incorporation into strongly dilated septa, x10.

4. Septal configuration in transverse view, the visibility of septal trabeculae, expansion of trabeculae, and development of dilation in the inner dissepimentarium. In addition, the development of "knobby", "pearly", or "yardarm" carinae in the septa.

Hexagonaria bassleri is uniformly cerioid, with straight intercorallite walls and dark epitheca that form a straight middle layer in the wall structure. The thickness of the walls varies somewhat from colony to colony (Plates 1 and 2), and in some is greatly thickened (reaching 0.5 mm thickness). Typically, this is in areas where septa are greatly thickened and develop a heavy pyramidal base (Plate 1, figures E, F), as in *H. hexagona*.

Hexagonaria bassleri thus resembles the type species of the genus and is characterized by calicinal features that are quite similar to those of *H. hexagona*. It has a peripheral flat calicinal platform and a central pit developed over the tabularium. This results in a wide dissepimentarium with rows of globular dissepiments that approach horizontality in the peripheral portion of the corallite but change rather sharply in the inner dissepimentarium into ovoid dissepiments that are steeply inclined (Plate 3, figures C, D). As is typical for disphyllids with long major septa, *H. bassleri* generally has rather regular development of axial and periaxial tabulae. ("Tabulae" is used herein to refer to all horizontal plates or platelets within the tabularium, as does the German noun *Boden*. Too much inconsistency and imprecision exists in the usage of the term "tabellae" to use it without a clear definition.) A sharp break between the tabularium and dissepimentarium reflects the presence of a deep calicinal pit on the upper surfaces of corallites.

In *Hexagonaria bassleri*, septal trabeculae are lath-like monacanthi identical to those in *H. hexagona*. There is variation within the sample from the Iowa population, but only in color and clarity of internal structure. In colonies with thin septa, monacanthine laths are generally light-colored, but these darken with greater dilation, and a feathery internal structure is then usually discernable. It is important to emphasize that the sharp lines seen in longitudinal section are boundaries between monacanthi, and not structures within them. This is typical for disphyllid corals. In *H. bassleri*, as in most disphyllids, the septal trabeculae are perpendicular to the orientation of the rows of dissepiments, and this reflects growth of septa perpendicular to the (former) topography of calicinal platforms. In longitudinal section, septal trabeculae (Plate 3, figures C, D) are generally oriented with inclined trabeculae at the intercorallite wall (making angles of 40 to 45°) and with trabeculae that become more inclined inward to the outer boundary of the tabularium. Variation between corallites is no greater than variation within corallites because trabeculae often show a marked bending in the inner dissepimentarium towards the corallite axis and may approach horizontality. However, trabeculae are sometimes straight and uniformly inclined towards the axis (Plate 3, figure D). This is associated with variation in the width of the dissepimentarium. A wide outer zone usually approaches horizontality and results in a strong inward bending of trabeculae as the innermost part of the dissepimentarium is approached. Narrow dissepimentaria apparently did not develop this same horizontal orientation, and trabeculae slope more uniformly throughout the septa.

Transverse sections of *Hexagonaria bassleri* show septal dilation and trabecular dilation (carination) to be highly variable within the Iowa population. There is a complete spectrum of septal dilation (Plates 1 and 2) from forms that show the typical disphyllid spindle-shaped or spear-shaped dilation (Plate 3, figure A), to thinly septate forms (Plate 2, figure F), to colonies in which septal dilation in the dissepimentarium results in straight-sided septa that are thick throughout the peripheral portion of the corallite (Plate 2, figure E). Septal trabeculae appear as

expanded lumpy portions of septa (Plate 2, figure F and Plate 3, figure A), either as greatly expanded trabeculae that form yardarm-like carinae (Plate 2, figure F) or as corrugations in the process of being covered over (smoothed) where septal dilation is extreme in the outer dissepimentarium (Plate 2, figure E). Thus the development of carination in this genus is seen as a step in the process of septal dilation, with dilation occurring first within trabeculae (in the outer dissepimentarium) and ending with the smoothing-over of septal flanks.

Hexagonaria oweni from the Frasnian Shell Rock Formation of Iowa also shows this character, with septal trabeculae expanded laterally as a stage of septal dilation but later engulfed by a smooth coating of stereome as a final stage of thickening (Plate 3, figures E, F). This type of swelling of trabeculae and development of yardarm-like carinae in *Hexagonaria* is much different from the development of yardarm carinae in *Heliophyllum* and related genera in the Cyathophyllina (Hill, 1981, p. 289). In these, trabeculae form first in the septa and are laterally expanded to form yardarms prior to the formation of septal portions between the carinae. In addition, carinae always remain distinct from intercarinal parts of septa and are not part of a process of septal dilation (Sorauf and Oliver, 1976, p. 331).

Taking the variability of *Hexagonaria bassleri* and related species into account, the genus may be diagnosed as follows (only a very limited synonymy is provided):

Genus HEXAGONARIA Gurich, 1896, emend.

Hexagonaria of Stumm, 1948.

Hexagonaria of Hill, 1956.

Argutastrea of Crickmay, 1962.

Hexagonaria of Pickett, 1967.

Disphyllum (in part) of Birenheide, 1978.

Hexagonaria of Birenheide, 1978.

Argutastrea of Hill, 1981.

Pseudohexagonaria of Kramer, 1982.

?*Cystihexagonaria* of Rohart, 1988.

Hexagonaria of Rohart, 1988.

not *Argutastrea* of Coen-Aubert and Lutte, 1990.

not *Pseudohexagonaria* of Coen-Aubert and Lutte, 1990.

Emended diagnosis.—Cerioid colonial corals of the Disphyllidae, characterized by clear differentiation of the tabularium and dissepimentarium, and thus by calicinal platform and axial pit. Long major septa extend well into the tabularium, although shorter minor septa do not, and septal dilation is spindle-shaped with maximum dilation in the inner dissepimentarium. Interference of (usually) long septa with formation of tabulae commonly, but not always, results in the development of axial and periaxial rows of tabulae. Monacanthine septal trabeculae of the disphyllid lath-like type show sharp boundaries with one another in longitudinal view. Dissepimentarium contains numerous globose dissepiments (generally five to ten per row). Where the dissepimentarium is wide, the outer dissepiments approach horizontality, but inner dissepiments are always steeply inclined towards the corallite axis. Septal trabeculae in longitudinal section form a structure that reflects the orientation of dissepiments and are perpendicular to calicinal surfaces. As a result, they form either a uniformly inclined cluster of trabeculae or a splay of trabeculae with axial inclination that increases to the innermost part of the dissepimentarium; where bending of trabeculae is seen. Reflexing of the calicinal platform and rows of dissepiments can result in the formation of upwardly bowed rows of dissepiments and the accompanying upward divergence of septal trabeculae.

Remarks.—The generic synonymy above is not meant to be all-

inclusive. Species with weakly swollen trabeculae and resultant irregular septa, or even with thin septa dilated only in the innermost part of the dissepimentarium, can be included in the genus *Hexagonaria*. Rohart (1988) and Coen-Aubert (1979) have included species with swollen trabeculae without specifically modifying the genus diagnosis. The genus is, then, a reasonably inclusive one. *Hexagonaria* thus defined need not be regarded as a "junk basket" name (*Sammelname* of Birenheide, 1978, p. 90). The genus *Pseudothexagonaria*, as diagnosed by Kramer (1982, p. 654), is in large part synonymous with the genus *Hexagonaria*, which includes many species with weak carination or carination that results from swelling of septal trabeculae. However, *Pseudothexagonaria*, as rediagnosed by Coen-Aubert and Lutte (1990, p. 23), depends less on carination (or lack of carination) for its definition, but is based on the presence of shortened major septa, open axial space, and septal dilation in the outer dissepimentarium rather than on the typical spindle-shaped septal dilation characteristic of *Hexagonaria*. Acceptance of this altered diagnosis may be the best method to differentiate genera closely allied to *Hexagonaria*; only further study of the pertinent species will prove its practicality.

Hexagonaria bassleri sometimes has incomplete septa in the outermost dissepimentarium where it becomes very wide. This is especially true where the corallites have undergone rapid budding (Plate 3, figure B). This raises a question regarding the validity of the genus *Cystihexagonaria* Rohart (1988, p. 273), which was proposed for specimens that resemble *Hexagonaria* but with a limited development of lonsdaleoid dissepimentaria. The former genus may indeed include a group of species that warrant use of the name, but such species have yet to be documented.

The possible inclusion in *Hexagonaria* of colonial disphyllids that have all or some corallites with reflexed calicinal platforms and a resultant upward spreading of septal trabeculae raises a similar question. Is it useful to retain the names *Paradisphyllum* Strusz (1965, p. 537) and *Martinophyllum* Jell and Pedder (1969, p. 735) for disphyllids that are analogous to *Disphyllum* and *Hexagonaria*, but with reflexed dissepimentaria and upwards spreading ("fanning") septal trabeculae?

The name "*Disphyllum*" is reserved in this report for species that are primarily fasciculate. This acknowledges the fact that some fasciculate species can form compact colonies with cerioid portions under some conditions, and can even form largely cerioid colonies when extremely favorable conditions prevail.

Argutastrea Crickmay (1960, p. 10) is also possibly synonymous with the genus *Hexagonaria* if its definition does not require the presence of yardarm carinae. However, Coen-Aubert and Lutte (1990, p. 20) have emphasized the following features in definition of the genus *Argutastrea*: (1) septa dilated in the dissepimentarium only; (2) long septa that reach to the corallite axis; and (3) great variability in the length of minor septa which are, however, generally short. If this revised definition of *Argutastrea* is followed, then the weakly carinate or non-carinate species of *Hexagonaria* may be recognized by their spindle-shaped septal dilation in the innermost dissepimentarium and outermost tabularium, by flat or gently arched rows of dissepiments, and by minor septa that generally reach the outermost tabularium.

The emended diagnosis of the genus *Hexagonaria* proposed above has relied heavily on understanding the variation seen within a few North American species of the genus, as well as within the small topotype sample from the Refrath area of Germany. This diagnosis will continue to be modified in the future, but it has the advantage of

removing the necessity that species included in the genus be "closely carinate" (e.g., Hill, 1981, p. 275). It also removes the need for a Subfamily Hexagonariinae and the grouping of carinate genera that are not closely related, as discussed below.

The Subfamily Hexagonariinae

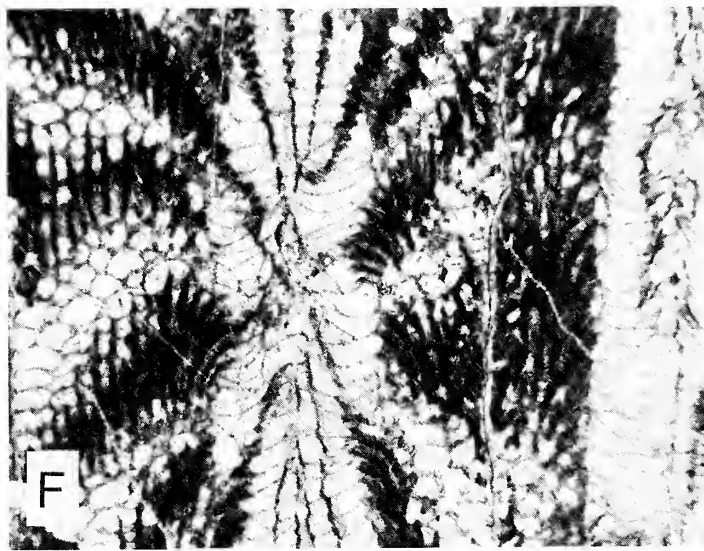
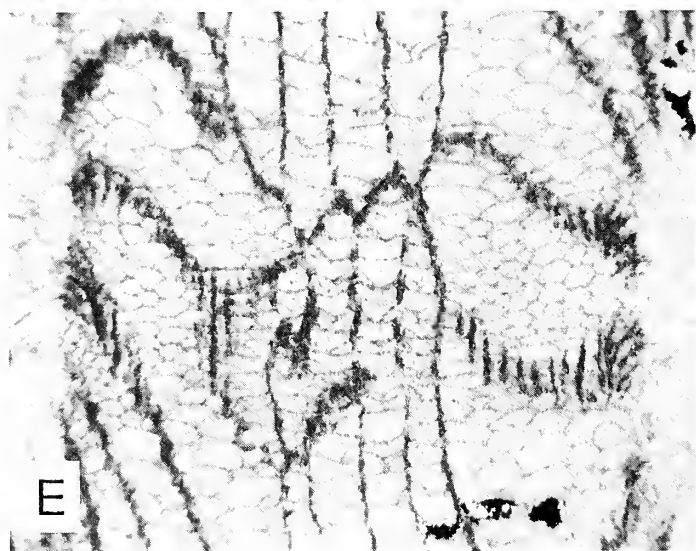
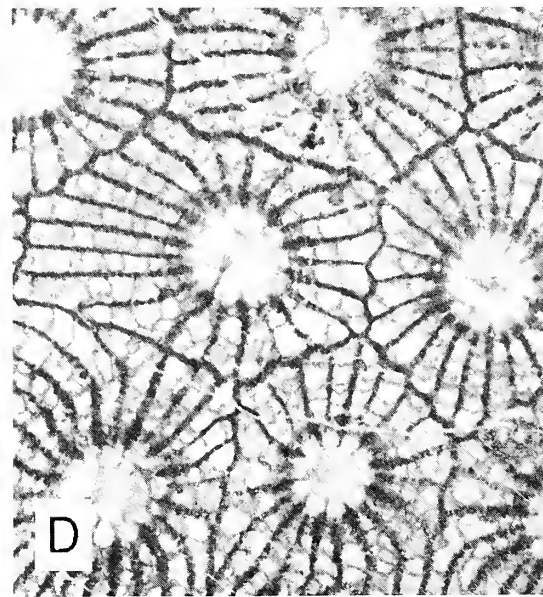
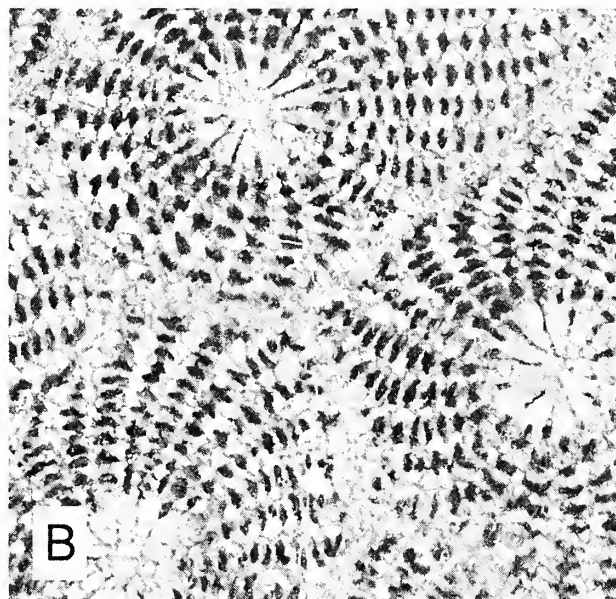
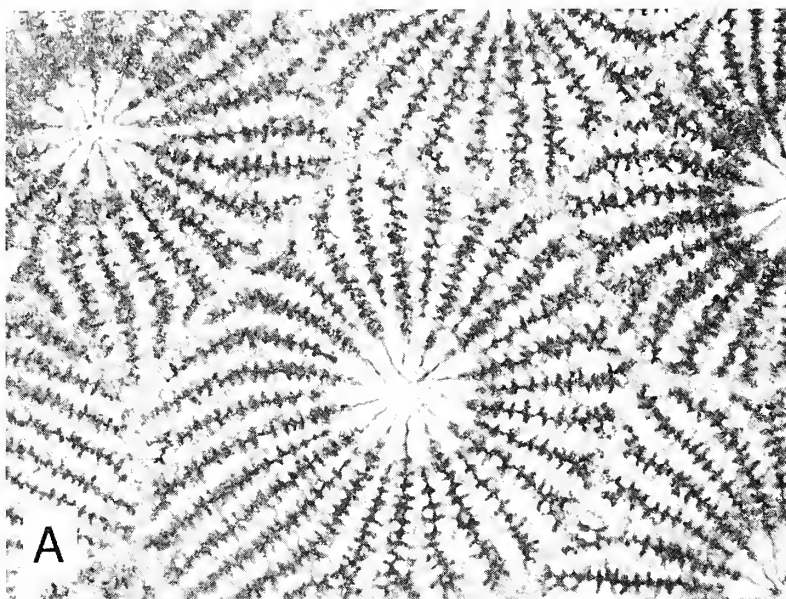
The Subfamily Hexagonariinae was recognized by Hill (1981, p. 275) as one of the subdivisions of the Family Disphyllidae. She included the genera *Hexagonaria*, *Haplothechia*, and *Marisastrum* within the subfamily, which she separated from other disphyllids by the presence of "closely carinate, long septa fusiform in transverse section; septal trabeculae ?tufted monacanth commonly in half-fans" (Hill, 1981, p. 275).

Regardless of how the carinate nature of *Hexagonaria* is viewed, there can be little question that the genus *Haplothechia*, which is closely carinate, as Hill (1981) noted, is not a near relative of *Hexagonaria*. It is more likely that neither *Haplothechia* nor *Marisastrum* should be classified with the Disphyllidae. However, Hill's (1981) statement that corals of all these genera are commonly carinate, have monacanthine trabeculae, and can have fanning septal trabeculae, is true. Most authors would agree with this generalization. However, all of these terms refer to morphological characters that are imprecisely and variably defined, or have only a superficial resemblance to similar features in other genera when they occur. Thus the association of these three seemingly important characters does not necessarily mean that the organisms are closely related.

In order to evaluate the Subfamily Hexagonariinae, it is germane to look at the relationship between the genera that are included in this group by Hill (1981). Although numerous features can be involved in such an evaluation, emphasis here is placed on the following: colony form and corallite size, type of septal trabeculae, configuration of trabeculae, and septal carination. *Marisastrum* is not included in this discussion.

Colonies of *Hexagonaria* are invariably cerioid (Plate 1). Large corallites have a tabularium diameter that varies from 3.5 to 6 mm and have approximately thirty-six to forty-two septa. *Haplothechia* is generally regarded as being characterized by the cerioid colonial form (Birenheide, 1978; Pedder, 1986). However, along with the topotype specimens of the type species *H. filiata* from Winterberg in the Harz Mountains, Germany, thamnasteroid corals also occur (Plate 4, figure C) that have the same diameter (approximately 2 mm), the same number of septa (mean of twenty-six), and septal carination that is identical to that of *H. filiata*. Should these individuals be assigned to *Haplothechia*, thus altering its generic diagnosis, or should they be assigned to *Kuangxiastraea*, a proposed thamnasteroid equivalent of *Haplothechia*? R.A. McLean (personal commun., 1990) has suggested that these individuals are best assigned to *Frechastraea carinata*. These decisions all depend on genus and species definitions. Should colonial form be uniform for each genus and for each species? This particular fauna, associated with the topotypes of *Haplothechia filiata*, needs to be studied in statistically significant numbers in order to define the amount of variation within the genus and its type species. The advisability of regarding the genera *Frechastraea* and *Haplothechia* as closely related forms is discussed below. The size difference in corallites of *Hexagonaria* and *Haplothechia* is pertinent to distinguishing the two genera, as many characters of rugose corals are related to corallite size.

Both *Hexagonaria* and *Haplothechia* have monacanthine trabeculae.



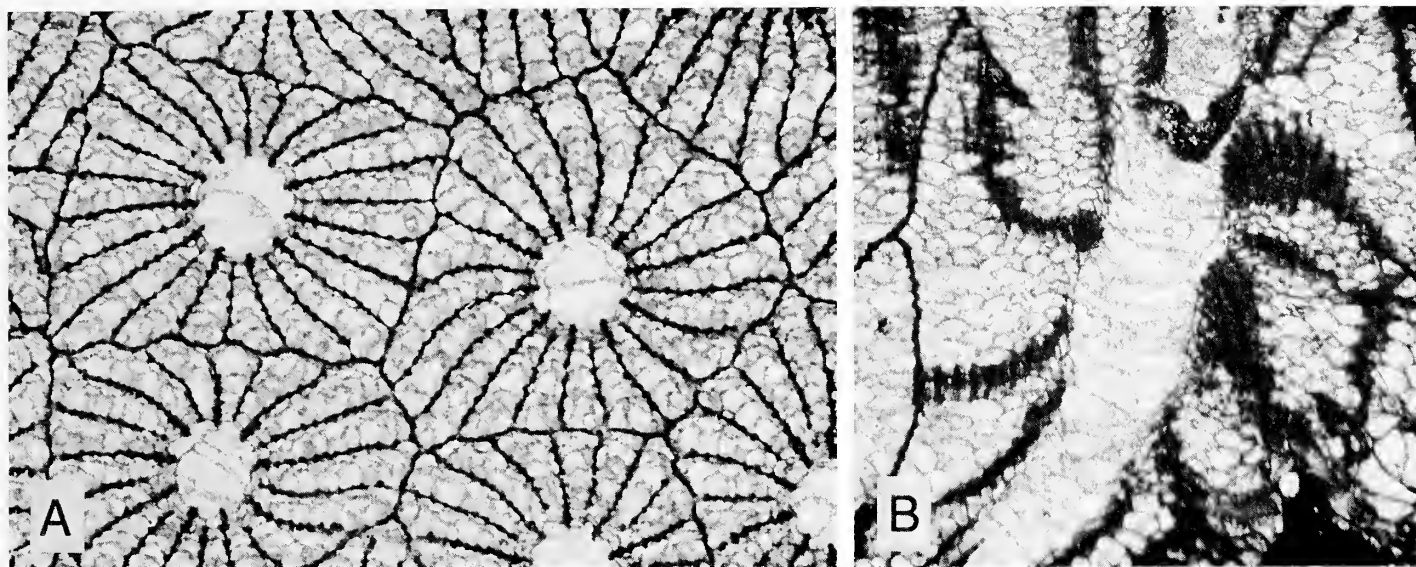


Plate 5. *Frechastraea goldfussi*, upper Frasnian, abandoned quarry, Neuville, Belgium (USNM 457066). *A*, Transverse section illustrating weak development of carination within pseudoceroid colony, x9. *B*, Longitudinal view of corallite with non-branching, non-fanning septal trabeculae and only a hint of intercalation of trabeculae in the inner dissepimentarium, x10.



Plate 4. *Haplothechia filiata* and *Frechastraea goldfussi*, Frasnian, Winterberg, near Bad Grund, Germany. *A-C*, *Haplothechia filiata*, topotypes, all x9, to illustrate variable development of intercorallite wall and uniform yardarm carinae. *A*, Cerioid colony with well-developed true cerioid wall (USNM 455877); *B*, ?Cerioid colony with sporadic development or diagenetic modification of epitheca in intercorallite wall (USNM 455878); *C*, Thamnasteroid colony lacking intercorallite walls, but with same diameter and number of septa as colonies in figures *A* and *B* (USNM 455879). *D*, *Frechastraea goldfussi*, transverse section, with pseudoceroid wall and lacking any development of septal carination, x9. *E-F*, *Haplothechia filiata*, topotypes, longitudinal sections, both x10. *E*, View of parts of two corallites illustrating slight elevation of inner dissepimentarium and branching and divergence of septal trabeculae in this position to form weak fan (USNM 457064); *F*, Colony with corallites with little development of fan-like divergence of septal trabeculae in inner dissepimentarium. Note in this individual that the minor septa are more likely to have a uniform increase in inclination axially, while major septa may show intercalation or branching of trabeculae in the inner dissepimentarium (USNM 457065).

However, the monacanth of *Hexagonaria* have a lath-like shape, as noted above, and are approximately 0.1 mm in diameter with a clear separation line between trabeculae (Plate 1, figures C, D). The monacanthine septal trabeculae of *Haplothechia* are much smaller in diameter and darker in color than those of the disphyllids. In longitudinal section, these commonly appear separated from one another (Plate 4, figures E, F), rather than being laths that abut one another. These are discrete monacanth that are similar to those in *Frechastraea*.

The arrays of trabeculae within septa of the two genera have been referred to as "fans" and "half-fans." This terminology has led to confusion. In disphyllids such as *Hexagonaria*, the lath-like trabeculae form a splay of monacanth that make an angle with the wall of the corallite. This angle increases towards the tabularium. The trabeculae maintain a position roughly perpendicular to the rows of dissepiments, and thus are most steeply inclined at the outer margin of the tabularium where dissepiments are inclined inward (adaxially). If the calicinal platform is reflexed (bowed upwards), then there may be some arching of the trabeculae. This has been called an "open trabecular fan," but the "fan" has little resemblance to trabecular fans in the Phillipsastreidae. In part, the configuration of the calicinal platform is dictated by environmental conditions, and this aspect of population variation needs more study before subfamilies can confidently be established on the basis of calicinal platform morphology and resultant trabecular configuration (e.g., the Paradisphyllinae, as utilized by Hill, 1981, p. 271, for genera with reflexed platforms).

Haplothechia has septal trabeculae that are also roughly perpendicular to the rows of small dissepiments in longitudinal sections of the corals. These monacanth tend to arch upwards and either branch or have intercalated monacanth inserted in the inner dissepimentarium, where arching of the dissepiment rows is most pronounced (Plate 4, figure E). Arching and development of horseshoe dissepiments in the inner dissepimentarium has not been seen in this genus. As a result(?), tight symmetrical fans are generally not present, as is typical of many phillipsastreids.

The carination in *Hexagonaria* is markedly different from that seen in *Haplothechia*. Carinae are variably developed in *Hexagonaria* and are closely related to dilation of trabeculae in many cases. In *Hexagonaria hexagona*, where septa are dilated in the inner dissepimentarium, one can see that laterally dilated septal trabeculae are involved. These are not uniformly distributed on the septa, are not present on all septa of corallites, and are not present in all corallites. Furthermore, as septa become dilated, stereome that was deposited on the flanks of the septa tends to obliterate the lateral projections of the carinae. Typically, carinate genera such as *Heliophyllum* or *Prismatophyllum* are characterized by attenuate septa with yardarm carinae that are formed first. The carinae are expressed as denticulations on the upper edge of the septa, and these are never smoothed over by stereome.

Hexagonaria, as described in recent reports, has commonly been regarded as a cerioid genus that has septal carinae and that includes species with variably swollen trabeculae. Several reports (Coen-Aubert, 1979; Rohart, 1988) have noted species of *Hexagonaria* that are characteristically "lightly carinate", and have figured photos of thin sections that illustrate corals with virtually no carinae, with slightly swollen trabeculae ("pearls" according to Rohart, 1988, p. 271), or with lumps ("nodes" of Coen-Aubert, 1979, pp. 7, 12) at the junctions of dissepiments and septa. It seems best to define *Hexagonaria* as a genus with disphyllid monacanth lath-like trabeculae that may be inflated to give a lumpy appearance to septa in transverse section, or that may even be laterally expanded to give yardarm-like carinae in some parts of the septa as part of the dilation process.

Haplothechia, on the other hand, is a coral that always contains evenly spaced and uniformly developed yardarm carinae distributed throughout all septa (in the dissepimentarium) in every corallite. This is seen in material figured by Scrutton (1967, p. 274), Pickett (1967, pp. 76, 81), Pedder (1986, pp. 653, 654), and Birenheide (1978, p. 240), and is shown in Plate 4 of this report. Septa are not dilated except in *H. ogwellensis* Scrutton (1967, p. 272), and with the exception of this species, carinae are never engulfed in septal stereome. Carination in *Haplothechia* and in *Hexagonaria* is so different that one might not wish to use the same term for both.

If *Haplothechia* and *Hexagonaria* do not closely resemble one another, and if *Hexagonaria* is a typical disphyllid, then where does *Haplothechia* belong? It is closely related to *Frechastraea*, and the two genera should be assigned to the Phillipsastreidae. A subfamily of phillipsastreids could include small-diameter corals with variable, perfectly or imperfectly formed fans of thin, dense monacanthine trabeculae, and variable development of specialized dissepiments or the horseshoe dissepiments that are characteristic of phillipsastreids.

Haplothechia and *Frechastraea* are corals of approximately the same size, have the same approximate number of septa, and have a similar development of small globose dissepiments in a relatively wide dissepimentarium. Both include species that lack horseshoe dissepiments (see Plate 4, figure E; and Plate 5, figure B, of *Haplothechia filiata* and *Frechastraea goldfussi*), although horseshoes occur in some species of *Frechastraea*. The species *H. filiata* and *F. goldfussi* have a very similar appearance in longitudinal section, as both have small-diameter, dark, dense monacanthine septal trabeculae. Both show branching and intercalation of trabecular segments in the inner dissepimentarium. In some species of *Frechastraea*, true phillipsastreid branching fans of septal trabeculae and horseshoe dissepiments occur. R.A. McLean (personal commun., 1990) notes that all individuals of seven species of *Frechastraea* that he has studied from western Canada show well-formed trabecular fans, at least in fortuitously placed thin sections. This has not been the experience of this author, but no attempt has been made to make thin sections that bisect these septal fans. It should be noted that the septal trabeculae illustrated in Plate 3, figures E and F, and in Plate 4, figure B, are the same size and thickness and have the same spacing between trabeculae. In the experience of the author, the development of trabecular fans is somewhat variable within *Frechastraea*, and thus the definition of the genus should not depend on their occurrence. Specimens of some species of *Frechastraea* have true phillipsastreid branching fans of septal trabeculae, and true horseshoe dissepiments may occur. Apparently, these features do not occur in *Haplothechia*. The figured specimens both have poorly developed fans.

Haplothechia is strongly and uniformly carinate, and the septa generally do not dilate, although carinae get fatter and increase the bulk of the septum. The wall in this genus is often a true epithecal wall, but the epithecal layer is sometimes discontinuous as a result of unknown diagenetic or unevaluated biogenic causes (Plate 4, figures A, B). There also may be an astreoid form of *Haplothechia filiata* among the topotype population from Winterberg near Bad Grund, Germany (Plate 4, figure C). *Frechastraea* does not exhibit yardarm carinae, such as those of *Haplothechia*, but often has dilated, swollen trabeculae in specimens with thin septa (Plate 5, figure A), which are similar to the "weak carinae" in *Hexagonaria*. The term "carinae" is best reserved for the yardarm type, where there is little question of the term's meaning. Nevertheless, there are expanding trabeculae in *Frechastraea*.

The colonial form is variable in *Frechastraea* and is possibly variable in *Haplothechia*. The majority of species are pseudocerioid, but Scrutton (1968, p. 231) and Birenheide (1978, p. 97) noted that both

these and astraeoid forms should be included in the genus. *Frechastraea* also has septa that expand at the outermost edge of the tabularium in some species to form an inner "wall." This is a feature peculiar to this phillipsastreiid genus and should not be confused with the aulos in the tabularium of genera in other families.

Haplothecia and *Frechastraea* have similar septal trabeculae and trabecular configuration; a similar general aspect of small, globose dissepiments; and common arching of the innermost part of the dissepimentarium. All of these features suggest that the two genera are closely related and should be classified within the Phillipsastreidae, perhaps with *Marisastrum*, in a separate subfamily of phillipsastreids. There are indications that there may be slightly carinate *Frechastraea* and, perhaps, both cerioid and astraeoid *Haplothecia*. If there are also pseudocerioid and astraeoid *Frechastraea*, then the genus name *Scruttonia* is unneeded. The name was proposed by Tcherepnina (1974, p. 102) for astraeoid colonies previously placed in *Frechastraea*. *Scruttonia*, along with *Frechastraea* and *Eridophyllum*, was placed in a Family Eridophyllidae (Tcherepnina, 1974, p. 102), on the basis of the development of an aulos in *Eridophyllum* and the typical development of a solid wall (perhaps resembling an aulos?) around the tabularium in some species of *Frechastraea* (and therefore also in *Scruttonia*). These genera (of the "Eridophyllidae") are not closely related. It does not seem logical to separate *Frechastraea* with pseudocerioid walls from identical corals with the thamnastraeoid colonial form. *Scruttonia* probably should be regarded as a junior synonym of *Frechastraea* rather than as a subgenus (as in Birenheide, 1990, p. 270). The genera *Haplothecia* and *Frechastraea* are alike in having a somewhat variable colonial form.

As a more general comment, it is unrealistic to assume either (1) that colonial form is unvarying at the genus level, or (2) that a genus name should be available for all possible colonial types within all branches of the Disphyllidae and the Phillipsastreidae.

Conclusions

Carination in *Hexagonaria* is concluded to be part of the process of septal dilation and is not analogous to carination in genera of the rugosan Suborder Cyathophyllina. The idea that *Hexagonaria* is composed only of species that are "closely carinate" should be abandoned. The concept of the genus should be kept broad enough to encompass corals with various degrees of lumpy or arm-like swelling of lath-like monacanthine septal trabeculae.

The Subfamily "Hexagonariinae" of the Disphyllidae, as diagnosed by Hill (1981) for cerioid disphylliids with uniform development of septal carinae, should be abandoned. *Hexagonaria* does not fit the description. *Haplothecia* and, perhaps, *Marisastrum* are more closely related to *Frechastraea* and belong within the Phillipsastreidae.

In general, it appears unlikely that a geographically widespread genus of variable corals, such as *Hexagonaria*, can be adequately defined on the basis of a single thin section of a neotype or, for that matter, on the basis of a type specimen and three topotypes. It should be no surprise that serious problems exist in the definition of cerioid disphylliid genera when such a key genus as *Hexagonaria* has not been adequately defined.

Acknowledgments

This report has benefitted greatly from reviews by W.A. Oliver, Jr.

and R.A. McLean, as well as the extremely thorough editing of E. Landing. R.A. McLean, in particular, raised questions concerning my treatment of Frasnian genera that I truly cannot answer satisfactorily without further research. I am grateful to all three for their help and intellectual stimulation.

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A late Pleistocene white whale (*Delphinapterus leucas*) from Champlain Sea sediments in northern New York

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Abstract

A fossil white whale (*Delphinapterus leucas*) is reported for the first time from New York State. The specimen, which on morphological evidence is believed to represent an old adult female, is a fairly complete skeleton excavated from clayey late Pleistocene sediments of the Champlain Sea in the town of Norfolk, St. Lawrence County. Fossils of *D. leucas* are rather common in Champlain Sea deposits in Canada. Clays associated with the specimen contain shells of the bivalve *Macoma balthica* that yield a radiocarbon date of $10,800 \pm 90$ yr B.P. Collagen from ribs of the whale date to $10,450 \pm 140$ yr B.P. These age determinations, which overlap at 1.6σ , suggest a stratigraphic position in the transition between the middle *Hiatella arctica* and final *Mya arenaria* phases of the Champlain Sea. A low diversity microfauna, characterized by the foraminiferan *Elphidium* sp. and the ostracodes *Candona* sp., *Cytheromorpha macchesneyi*, and *Heterocyprideis sorbyana*, indicates a nearshore, brackish, cold-water environment during deposition of the whale specimen.

Introduction

On 23 August 1987, Duane V. Pelkey discovered a few large bones in clayey sediments he had excavated with a backhoe while constructing a farm pond on Ben LaRue's property in the town of Norfolk, 10 km southeast of Massena, St. Lawrence County, New York ($44^{\circ}51'25''N$, $74^{\circ}52'10''W$; USGS Brasher Falls 7 1/2-minute Quadrangle). During the next several days, his son Duane M. Pelkey

recovered many additional bones by sorting carefully through the back-dirt by hand and with 1/4" sieves. After the bones were cleaned, WTK and DMP showed the specimen to C.R. Harington of the National Museum of Canada (now Canadian Museum of Nature), Ottawa, who identified it as *Delphinapterus leucas*, the white whale or beluga. The fossil was first reported in the scientific literature by Kirchgasser et al. (1989). This report confirms the identification, describes and compares the specimen, and outlines its stratigraphic, chronologic, and biogeographic contexts.

The specimen

The sixty-three complete or partial fossil bones (Figures 1, 2) are repositied in the New York State Museum Vertebrate Fossil collection as NYSM 5095. After the removal of all sediment, each bone was slowly dried and then immersed in polyvinyl acetate to harden it and to provide long-term protection against splintering. The specimen consists of the following bones (osteological nomenclature follows that of Rommel, 1990): partial basicranium (exoccipital, basioccipital, pterygoid); partial braincase (supraoccipital, exoccipital, nasals, ectethmoids, mesethmoid); left and right fused maxilla/premaxilla; left squamosal; left frontal; nearly complete left and right dentaries; six isolated dentary teeth; axis; cervical vertebra 7; thoracic vertebrae 1, 2, 5-10; lumbar vertebrae 1-6, 8-10; caudal vertebra 9; twenty partial or complete ribs (including six sternal ribs and two floating ribs); most of the sternum; proximal portion of the right scapula; and a carpal (intermedium). Had the specimen been discovered and excavated in situ, perhaps the entire

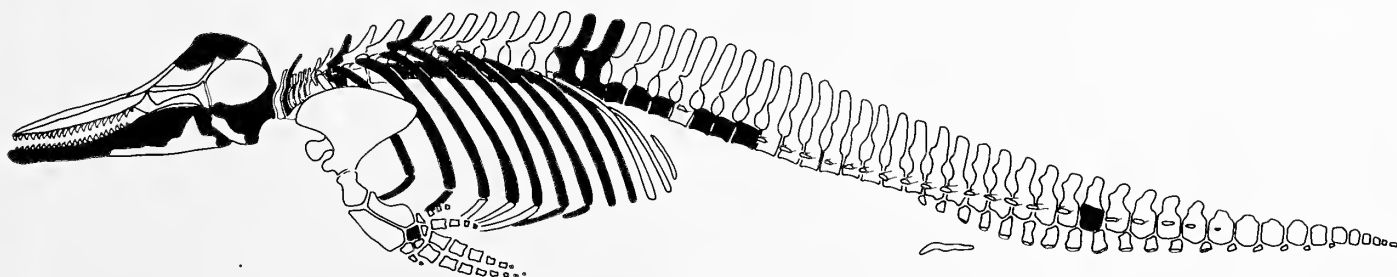


Figure 1. *Delphinapterus leucas*. Shaded bones are those represented in the Norfolk specimen of *D. leucas*, NYSM 5095. Skeletal outline is based upon a specimen of the delphinid *Tursiops truncatus* from Rommel (1990). Figure does not include elements from the animal's right side.

skeleton would have been recovered. Except for slight rounding on the transverse and dorsal processes of certain vertebrae, NYSM 5095 retains all of the anatomical detail of a modern specimen. This suggests that the specimen was subjected to very little post-mortem transport.

The basicranium of NYSM 5095 is remarkably similar in size and shape to a fossil specimen of *Delphinapterus leucas* in the Paleobiology Division, Canadian Museum of Nature (NMC 6842). This specimen was discovered about 1870 at Cornwall, Ontario, and is the locality nearest to Norfolk of all previous late Pleistocene records of *D. leucas*. The various cranial elements are more completely fused in NYSM 5095 than in any of the modern U.S. National Museum of Natural History (USNM) specimens. The cranial elements of NYSM 5095 possess the distinctive bilateral asymmetry that characterizes *D. leucas*. The dentaries of NYSM 5095 are similar in size and shape to those of another fossil specimen of *D. leucas* collected in 1906 near Pakenham, Ontario (NMC 21336). The dentaries of NYSM 5095 are qualitatively inseparable from those of all modern specimens of *D. leucas* in the USNM. Measurements of selected individuals from the USNM collection are summarized in Table 1.

The cervical vertebra and the first two thoracic vertebrae of NYSM 5095 display irregularities (spurs and porous degenerative bone) that probably indicate arthritis and advanced age. All of the vertebral epiphyses are completely fused in NYSM 5095, and this also indicates an old individual. The six heavily worn lower teeth are compatible with the suggestion that this specimen represents an old individual, although tooth wear alone is not a reliable indicator of age in *Delphinapterus leucas* (J.G. Mead and S. Rommel, personal commun., 1990). Analysis of the growth layers of mandibular teeth has been used to determine age in *D. leucas* (Brodie, 1969; Hansen et al., 1990), but this technique was

inconclusive in NYSM 5095. Two standard sections of 200 microns thickness from one mandibular tooth could not be interpreted because crown wear had eliminated an unknown number of growth layers (W. Hoek, personal commun., 1989). White whales generally live about twenty-five to thirty years (Nowak and Paradiso, 1983, p. 898). The age of NYSM 5095 probably is in that range.

Adult males of *Delphinapterus leucas* are larger on average (total length ca. 335-485 cm) than females (ca. 300-400 cm) (Nowak and Paradiso, 1983, p. 897). By a comparison of the lengths of the dentary and vertebrae of NYSM 5095 to those of a modern individual of known length (Tables 1, 2), the total length of NYSM 5095 is estimated to have been about 380 cm. Although this length is in the range of overlap between males and females, NYSM 5095 most likely is a female, particularly in view of its advanced age as indicated by the high degree of fusion of the skull elements and vertebral epiphyses. In addition, the relatively gracile nature of most of the skeleton suggests a body much smaller than indicated by length measurements alone. NYSM 5095 also resembles modern females rather than males in its relatively slight occipital and sagittal crests.

Stratigraphy and chronology

Sedimentary setting

The surface elevation of the locality is 82 m. None of the fossil whale bones were found in situ because the excavation was flooded shortly after the bones were noticed in the backdirt. Subsequently, the walls of the excavation collapsed, and this prevented recovery of more bones. Nevertheless, on the basis of correlation of sediment clinging to

Table 1. Measurements (in mm) of various skull elements in *Delphinapterus leucas*. NYSM 5095 is the late Pleistocene specimen from Norfolk, New York. USNM 571021, modern specimen from Maine (adult male, length 399 cm). USNM 504673, modern specimen from Newfoundland (adult female, length 343 cm). USNM 504767, modern specimen from Manitoba (subadult female, length 318 cm). L=left; R=right. Ratios (%) are calculated only for the length of the dentary because, on the basis of our research, other individual measurements seem to bear little, if any, relation to overall length of the entire animal.

	NYSM 5095	USNM 571021	USNM 504673	USNM 504767	% 5095/ 571021	% 5095/ 504767
Length of L dentary	386	461	—	352	83.7	109.7
Length of R dentary	395	467	—	—	84.6	—
Max. width foramen magnum	53.8	56.4	50.7	—	—	—
Max. depth foramen magnum	58.0	51.8	56.6	—	—	—
Max. width occipital condyles	138	152	124	—	—	—
Length of zygomatic process of L squamosal	90.4	97.1	86.2	86.0	—	—
Max. width across L maxilla/premaxilla, just anterior to blowhole	130	152	121	120	—	—
Max. width across R maxilla/premaxilla, just anterior to blowhole	139	157	127	—	—	—
Least width from blowhole across L maxilla	71.8	69.0	67.6	—	—	—



Figure 2. Selected skeletal elements represented in NYSM 5095. *A*, Lateral view of right dentary. *B*, Ventral view of basicranium (basioccipital, exoccipital), showing occipital condyles and foramen magnum. *C*, Dorsal view of maxilla/premaxilla and blowhole. *D*, Lateral view of a series of dentary teeth with occlusal surfaces on top and roots on the bottom. Each scale=10 cm.

the bones and the observations of the backhoe operator, it is thought that the fossil whale bones came from grey, sandy clays at or near the base of the 3.0 m-deep pit. The locality is a sand and gravel pit with underlying clays on the flank of an elongate till-ridge that trends north-east-southwest (see Carl, 1978).

Long-term preservation of the whale bones might be attributed to burial in oxygen-poor, impermeable clays rather than in the sands and gravels that typify the crests of till-ridges of the St. Lawrence Lowland. These till-ridges (Figure 3) are believed to have formed beneath the ice when the glacial till or ground moraine was pushed and molded into wave-like forms during southward advances of the ice front at about 12,800 yr B.P. (Carl, 1978). Subsequently, the till-ridges and surrounding valleys were flooded by glacial Lake Iroquois and successive lower-elevation lakes that formed from glacial meltwater and runoff after the retreat of the Laurentide ice sheet into southern Ontario and Quebec. The lakes developed between the receding ice front to the north and the Adirondack upland to the south beginning about 12,500 yr B.P. (Clark and Karrow, 1984). Final drainage was through an outlet around Covey Hill, near Malone, New York, prior to the invasion of the Champlain Sea, which occurred about 12,000 or 11,800 yr B.P. (MacClintock and Stewart, 1965; Denny, 1974; Rodrigues and Richard, 1986; Rodrigues, 1988). The Champlain Sea was an arm of the Atlantic Ocean that flooded the ice-depressed St. Lawrence and Champlain Lowland

(Figure 4). The sea retreated from the region at about 10,000 yr B.P. (Rodrigues, 1988) as the crust rebounded in response to the removal of ice.

Wave and current action in the glacial lakes reworked and winnowed the sediments on the crests of the till-ridges and left behind the sorted, well-drained (and commercially valuable) sands and gravels that characterize the higher ground of the region today (Figure 3). Fine-grained silts and clays winnowed from the till-ridges were deposited in the quiet deeper water adjacent to the ridges to form horizontal layers of lake silts and clays (rhythmites, or varved clays) that record an alternating pattern of differential deposition during the winter, when ice covered the lakes, and during the ice-free summer. These relatively impermeable, poorly drained sediments underlie the low wetlands of the region.

The reworking of sediments by waves and currents continued when the marine waters of the Champlain Sea inundated the region and replaced the last of the freshwater lakes. Fossiliferous marine clays (formerly referred to as the Massena-Leda clay) and sands were deposited over the lake sediments in low areas between the ridges. Locally, the shells of marine bivalves can be found scattered in the winnowed till along the ridge crests. At the time of deposition of the whale and associated bivalves at Norfolk, the nearest southern limit of the marine shoreline was near Norwood, New York (44°45'N, 75°00'W; see Pair et al.,

Table 2. Length (in mm) of the vertebral centrum in *Delphinapterus leucas*. Assignment of fossils to a specific vertebra is based upon morphological rather than mensural comparisons with USNM 571021. NYSM 5095 is the late Pleistocene specimen from Norfolk, New York. USNM 571021 is a modern specimen from Maine (adult male, length 399 cm).

	NYSM 5095	USNM 571021	% 5095/571021
Axis	57.1	60.4	94.5
5th thoracic	61.4	64.6	95.0
6th thoracic	66.5	70.9	93.8
7th thoracic	71.0	74.6	95.2
8th thoracic	76.0	78.4	96.9
9th thoracic	80.9	82.7	97.8
10th thoracic	84.3	85.4	98.7
1st lumbar	90.8	90.3	100.5
2nd lumbar	92.7	94.0	98.6
3rd lumbar	95.9	96.2	99.7
4th lumbar	101.7	104.5	97.3
5th lumbar	104.4	105.2	99.2
6th lumbar	105.9	106.7	99.2
8th lumbar	109.0	106.6	102.2
9th lumbar	103.8	106.1	97.8
9th caudal	59.9	59.4	100.8
Length of all 16 vertebrae	1361.3	1386.0	98.2

1989). The difference in modern elevation between the Norwood shoreline and the Norfolk site suggests that water was about 51 m deep at the site when the whale bones were deposited. This calculation may not be accurate, however, because it does not consider the effect of post-glacial rebound, which most likely was not uniform between Norwood and Norfolk.

Biostratigraphy

The sediments associated with the whale yield a low-diversity benthic microfauna, including the bottom-dwelling foraminifera *Elphidium* sp. A count of two hundred and thirty-four ostracodes from a sample of this sediment by T.M. Cronin, U.S. Geological Survey (personal commun., 1988), reveals the following species (with number of identified specimens in parentheses): *Candona* sp. (144), *Heterocyprideis sorbyana* (47), *Cytheromorpha macchesneyi* (38), *Sarsicytheridea puntillata* (3), *S. bradii* (1), and *Cytheropteron* sp. (1). These forms occur today in arctic and subarctic seas and estuaries. All are marine-brackish species except *Candona* sp., a freshwater form that indicates low salinity (i.e., brackish water of ca. ≤ 5 ppt). Considered as an assemblage, the ostracode fauna indicates a cold (bottom water temperature between -1.5° and $+4^{\circ}\text{C}$), nearshore, brackish environment at the time and place of deposition of the whale specimen. This assemblage compares well with Biofacies I of Cronin (1979).

Bivalves associated with the whale include abundant shells of *Macoma balthica*, as well as scattered specimens of *Hiatella arctica*.



Figure 3. Till-ridge in a sand and gravel pit (not the fossil site, which is destroyed), Norfolk, New York.

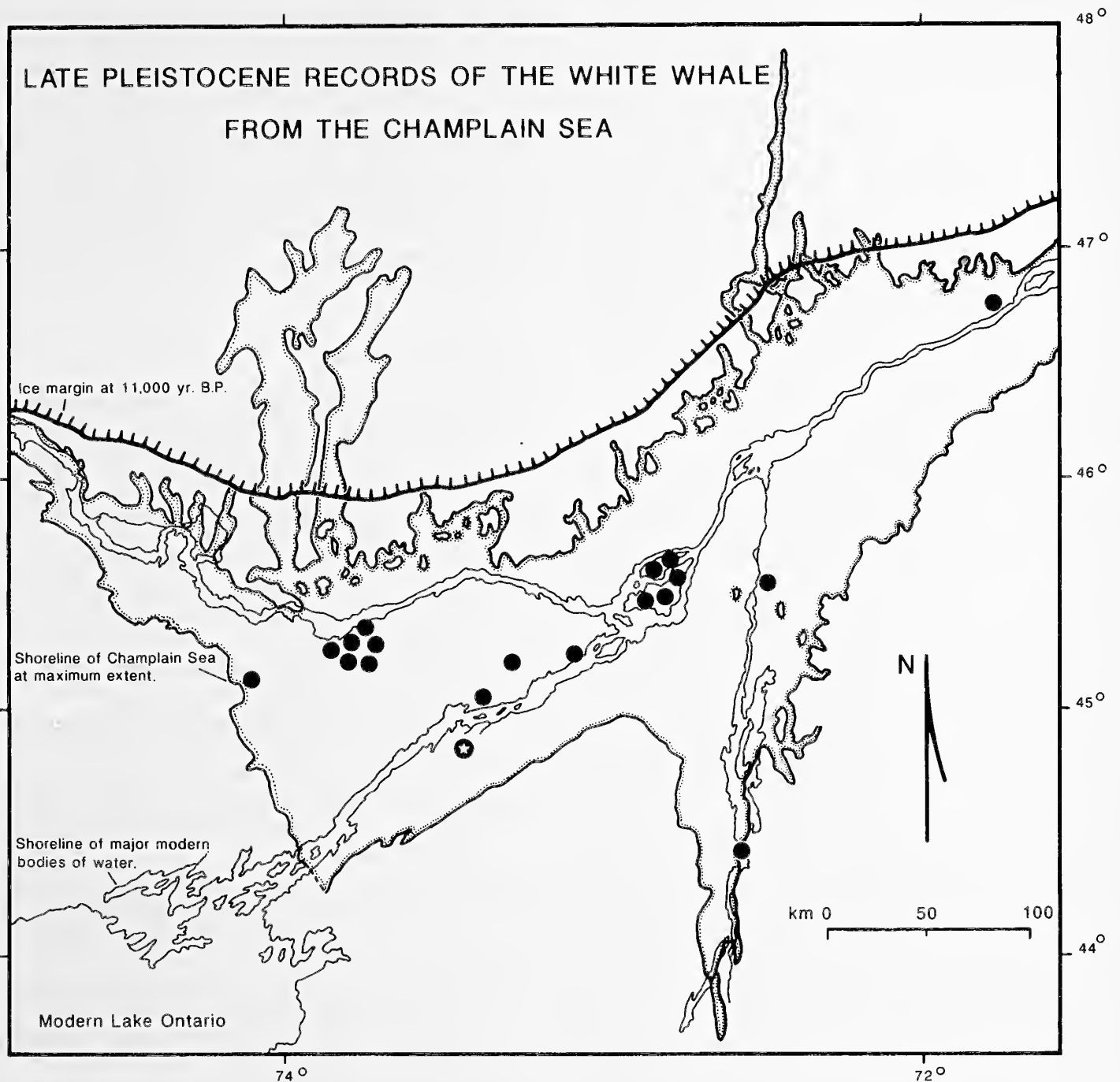


Figure 4. The Champlain Sea near its maximum extent. Shows all previous records of *Delphinapterus leucas* (filled circles) and the new record from Norfolk, New York (star within circle). Modified from Harington and Occhietti (1988) and Harington (1989).

This bivalve fauna and the microfauna described above are similar to those of the upper part of the section near Navan, Ontario (site 8), in the western Champlain Sea basin (Rodrigues and Richard, 1986; Rodrigues, 1987). Brackish water at the Norfolk site is suggested by the specimens of *M. balthica*, which are smaller (mean length 13.3 mm, range 7.4-18.5 mm, $n=99$) than specimens of *M. balthica* collected from Champlain Sea sediments indicative of more open, deeper marine waters, such as those that occur to the northeast along the St. Lawrence River and northern Champlain Valley (Goldring, 1922) and in the west-

ern Champlain Sea basin in Ontario (Rodrigues, 1987). The temporal range in the western Champlain Sea basin for *M. balthica* is ca. 12,400-10,400 yr B.P., whereas that for *Hiattella arctica* is ca. 11,500-10,000 yr B.P. (Rodrigues, 1989, p. 161). These age ranges are compatible with the ages determined for the Norfolk whale.

Radiocarbon dates

Shells of *Macoma balthica* (ca. 80 gm) from the Norfolk site yielded a radiocarbon (^{14}C) age of $10,800 \pm 90$ yr B.P. (Beta-25253, corrected

for $^{13}\text{C}/^{12}\text{C} = -2.2$ ‰ (PDB). Purified collagen from 540 gm of ribs (not treated with polyvinyl acetate) from the Norfolk whale yielded a ^{14}C age of $10,450 \pm 140$ yr B.P. (Beta-25252; corrected for $^{13}\text{C}/^{12}\text{C} = -18.7$ ‰ (PDB)). The collagen-based ^{14}C age is similar to, and statistically inseparable from, two others determined on bones of *Delphinapterus leucas* from Champlain Sea sediments, namely $10,420 \pm 150$ yr B.P. from Foster Sand Pit (south of Ottawa) and $10,400 \pm 80$ yr B.P. from the Pakenham site, Ontario (Harington and Occhietti, 1988, pp. 50, 53). The two age determinations from the Norfolk site overlap at 1.6 σ . The possibly slightly older age determined from the bivalves as compared to the bone might reflect minor contamination with "dead" inorganic carbon in the bivalve shells. These age determinations suggest a stratigraphic position of the Norfolk whale in the transition between the middle *Hiattella arctica* and final *Mya arenaria* phases of the Champlain Sea as defined by Cronin (1977, 1981).

Discussion

Although eighteen other specimens of *Delphinapterus leucas* have been reported from Champlain Sea sediments (Harington and Occhietti, 1988; Harington, 1989; Figure 4, herein), this is the first one from the southwest margin of the sea in New York State. Aside from *D. leucas*, which constitutes about 80% of the whale specimens recorded from Champlain Sea sediments, the marine mammal fauna of the Champlain Sea included the humpback whale (*Megaptera novaeangliae*), bowhead whale (*Balaena mysticetus*), harbor porpoise (*Phocoena phocoena*), ringed seal (*Phoca hispida*), harp seal (*Phoca groenlandica*), harbor seal (*Phoca vitulina*), and bearded seal (*Erignathus barbatus*) (Ray, 1983; Harington, 1977, 1989; Harington and Occhietti, 1988).

Today the white whale is primarily an arctic species, with a worldwide population of 60,000 to 80,000 and a circumpolar range centered in the Arctic Ocean and extending to adjacent seas, estuaries, and large rivers as far south as the Sea of Okhotsk, Bering Sea, Gulf of Alaska, Hudson Bay, and the lower (eastern) St. Lawrence Estuary (Nowak and Paradiso, 1983, p. 897). Individuals are known to stray as far south as Japan, Washington, New Jersey, Ireland, Scotland, the Rhine River, and the Baltic Sea (Nowak and Paradiso, 1983, p. 897). Of greatest pertinence to the New York fossil is the isolated resident population of white whales in the St. Lawrence Estuary. The western limit of this population is about 570 km ENE of the New York fossil locality. The St. Lawrence population has been estimated at 5,000 at the beginning of this century, 1,200 when commercial hunting ended in the 1950s, and only about 500 animals in the 1970s through 1985 (Sergeant and Brodie, 1969; Sergeant and Hoek, 1988). With the cessation of both commercial and sport hunting, the most recent population decline has been attributed, at least in part, to chemical pollutants, particularly organochlorines. More than 10,000 years after what might have been their peak of abundance, we risk today the complete loss of white whales in the St. Lawrence region.

Acknowledgments

We thank Duane V. Pelkey for alerting us about the fossils and W. Taylor, D. Straight, and W. LaRue for help in collecting them. We especially thank Ben LaRue for graciously donating the specimen to the New York State Museum. C.R. Harington, W. Hoek, J.G. Mead, C.W.

Potter, C.E. Ray, and S. Rommel generously shared their knowledge of cetaceans and allowed us to study specimens under their care. T.M. Cronin kindly identified and interpreted the ostracodes. For comments on the manuscript, we thank T.M. Cronin, C.R. Harington, E. Landing, N.G. Miller, and C.E. Ray. S. Bresett, J. Gruppe, J. Kralick, S. Miles, S. Patrick, and A. Russell, former students of WTK, assisted in laboratory preparations. R. Bitely provided the photograph for Figure 3, and C. Supkis photographed the bones in Figure 2. Figures 1 and 4 were prepared by P. Kernan. This is contribution number 665 of the New York State Museum and Science Service. DWS supplied \$150 toward publication of this report from the Zoology Research Fund of the University of the State of New York.

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Brachiopod and trilobite biofacies of the Rochester Shale (Silurian, Wenlockian Series) in western New York

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Abstract

The brachiopod and trilobite faunas of the Rochester Shale (Silurian, Wenlockian) of western New York comprise distinct biofacies that are both depth-related and controlled by lithofacies. Brachiopod biofacies in the west side of the Appalachian Basin (Niagara Falls region) include the *Atrypa-Howellella* (down to storm-wave base), *Striispirifer* (near and just below storm-wave base), and *Amphistrophia-Stegerhynchus* (below storm-wave base) Biofacies. The east side of the basin (Sodus Bay region) contains the *Whitfieldella-Rhynchotreta* (down to storm-wave base), *Eospirifer-Dalejina* (near and just below storm-wave base), and *Amphistrophia-Stegerhynchus* (below storm-wave base) Biofacies. The trilobite fauna of the Rochester Shale is part of a very extensive *Dalmanites* Magnabiofacies, which spans a wide variety of environments. It is subdivided into four biofacies. The western trilobite biofacies include the *Bumastus* (down to storm-wave base), *Arctinurus* (near and just below storm-wave base), and *Trimerus* (below storm-wave base) Biofacies. The east side of the basin contains the "*Calymene*" (down to just below storm-wave base) and *Trimerus* (below storm-wave base) Biofacies. Both brachiopod and trilobite diversity in the Rochester Shale decreases with increased depth, but trilobite abundance remains relatively constant.

Introduction

Despite an extensive literature on Silurian brachiopod-dominated, level-bottom communities (Ziegler, 1965; Ziegler et al., 1968; Calef and Hancock, 1974; Boucot, 1975; Lawson, 1975), relatively few studies have focused on the distributional paleoecology of trilobites (see Thomas, 1979; Mikúlic and Watkins, 1981). The purpose of this study is to examine the distribution of both the brachiopod and the trilobite faunas of the Silurian Rochester Shale, with emphasis on the trilobites.

The Rochester Shale

The Rochester Shale (Silurian, Wenlockian Series, Clinton Group) of southern Ontario and western New York was the first rock unit to be named in North America (Hall, 1839). In the Niagara and Rochester areas, it rests on the Irondequoit Limestone and is capped by the Decew Dolostone (Figure 1). In the Sodus area, the Rochester Shale also rests

on the Irondequoit but is overlain by an argillaceous, resistant limestone bed herein referred to as the "Glenmark Bed" (Brett, personal comm., 1986), named after the village of Glenmark, where this bed forms the cap of a waterfall. The Rochester Shale has been known for over 150 years to contain a well-preserved and diverse trilobite fauna, and was well-represented in the first monograph published on North American trilobites by Jacob Green (1832). Hall (1852) and Grabau (1901) discussed the entire Rochester Shale fauna, but it has received very little attention since that time.

Stratigraphic and sedimentological features of the Rochester Shale have received considerably more attention than its paleontology. As part of more comprehensive studies of New York and Ontario Silurian rocks, the Rochester Shale has been examined in the context of quantitative petrology (Alling, 1936, 1946), stratigraphy (Bolton, 1957; Gillette, 1940, 1947), and depositional environments (Thusu, 1972).

More recently, Brett (1978a, 1978b; Brett and Eckert, 1982) has studied the rich echinoderm fauna and the sedimentology and stratigraphic relations of the Rochester Shale (Brett, 1982, 1983a, 1983b). Brett demonstrated that the Rochester Shale was not deposited under uniform depth conditions, but recorded a series of oscillations in relative water depth and, by inference, transgressions and regressions. On the basis of lithologic changes induced by these cyclic depth variations, Brett (1983b) subdivided the Rochester into a lower Lewiston Member and an upper Burleigh Hill Member. In the Rochester area, the very dolomitic shales of the Gates Member (originally proposed by Chadwick, 1918) replace most of the Burleigh Hill Member and compose the upper third of the section. The Lewiston Member is, in turn, subdivided (Brett, 1983b) into five easily traceable subunits ("A" through "E"). On the basis of the nature and frequency of storm-event beds, Brett (1983a) determined that the central subunit (Lewiston "C") represents the deepest part of the transgression-regression cycle of the lower Rochester Shale.

Study area

A 200 km-long segment of the outcrop belt was examined in western New York during this study (Figure 2). Three major sections were selected for detailed sampling: the Niagara River Gorge section at Niagara Falls (Figure 3), the Genesee River Gorge section at Rochester, and a section exposed along an unnamed tributary of Sodus Creek near North Rose. These sections were measured in detail and were divided

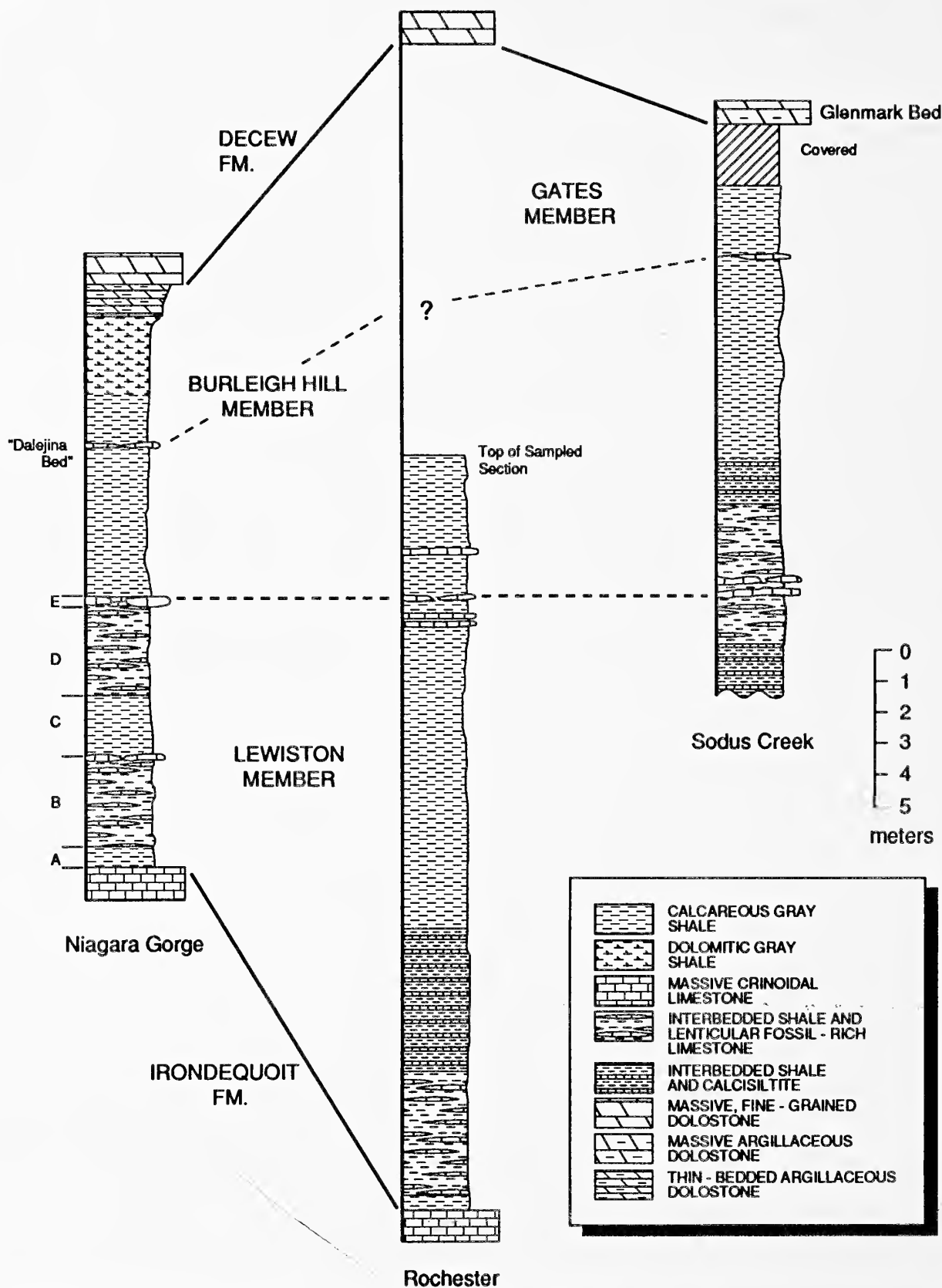


Figure 1. Stratigraphic sections of the Rochester Shale at three New York State localities. Height of the Decew Dolostone above the Lewiston "E" at Rochester is inferred by comparison to the Gates Canal section, 9 km to the east.

into 0.5 m and 1.0 m intervals. Each interval was then systematically sampled and examined from top to bottom. Each 1.0 m sample interval represented approximately 0.09 cubic meters of rock. An attempt was made to identify every fossil fragment to species within each interval. Absolute abundance and other data were recorded for the trilobite material, and relative abundance was recorded for all other fossil groups. Representative samples from each interval were taken back to the lab for preparation, closer examination, and photography.

The sample data were charted on three spindle diagrams (Figures 4-6) to allow comparison of trilobite distribution patterns with those of other faunal elements, particularly the brachiopods. Reconnaissance sampling of key intervals was also undertaken at more than twenty additional localities, and extensive collecting was done at many of the more important trilobite-bearing occurrences. Type and non-type material from the collections of the Royal Ontario Museum (Toronto), New York State Museum (Albany), Buffalo Museum of Science, and University of Rochester was examined. Material from the private collections of J. Eckert, G. Kloc, and K. Smith was also examined.

The data obtained by sampling the trilobite and non-trilobite faunas were compared to those derived from earlier described transgressive-regressive cycles. From this, it is possible to ascertain whether these depth changes had any effect on the composition of the fauna within a superficially homogeneous, shaly lithology. Brachiopod and trilobite biofacies are defined in the course of this study.

Paleoecologic reconstruction of the Rochester Shale

Fragments of the trilobite *Dalmanites limulus* are some of the most abundant fossils throughout the Rochester Shale. Three brachio-

pod species, *Stegerhynchus neglectum*, *Coolinia subplana*, and *Amphistrophia striata*, approach *Dalmanites* in both their abundance and wide distribution. The entire Rochester Shale could therefore be assigned to a "*Dalmanites* Biofacies" or a "*Stegerhynchus* Biofacies." However, the eurytopic nature of this dalmanitid trilobite and rhyconellid brachiopod would render such biofacies descriptions relatively useless to all but the most general, large-scale biostratigraphic or paleoecological studies. It would lump together relatively unfossiliferous, shallow-water carbonates; highly diverse, shallow-water, wave-agitated bryozoan biostromes; brachiopod shell pavements that represent various depths; and deep-water, barren mudstones. This wide variety of environments (all present within the Rochester Shale as well as in many other *Dalmanites*-bearing Silurian formations) results in a relatively high diversity of trilobite genera in the Rochester Shale (approximately twenty, each represented by a single species), most of which are fairly stenotopic (Tetreault, 1987). By means of these other, often less-common genera, the fossil assemblages described herein can be subdivided into more useful groups that can then be used in both paleoecological analyses and comparisons with other faunas.

Tempestite proximality and taphonomic attributes of collections provide criteria for establishing bathymetry (e.g., Speyer and Brett, 1986; Brett et al., 1986; Parsons et al., 1988). It has also been demonstrated that Silurian and Devonian brachiopod biofacies of New York State are broadly depth-related in their distribution (Brett, 1983a; Savarese et al., 1986). By integrating these two approaches, an environmental framework and basin bathymetry can be established for the Rochester Shale from the distribution of brachiopod biofacies and the number and type of storm beds. Brachiopod biofacies are defined from

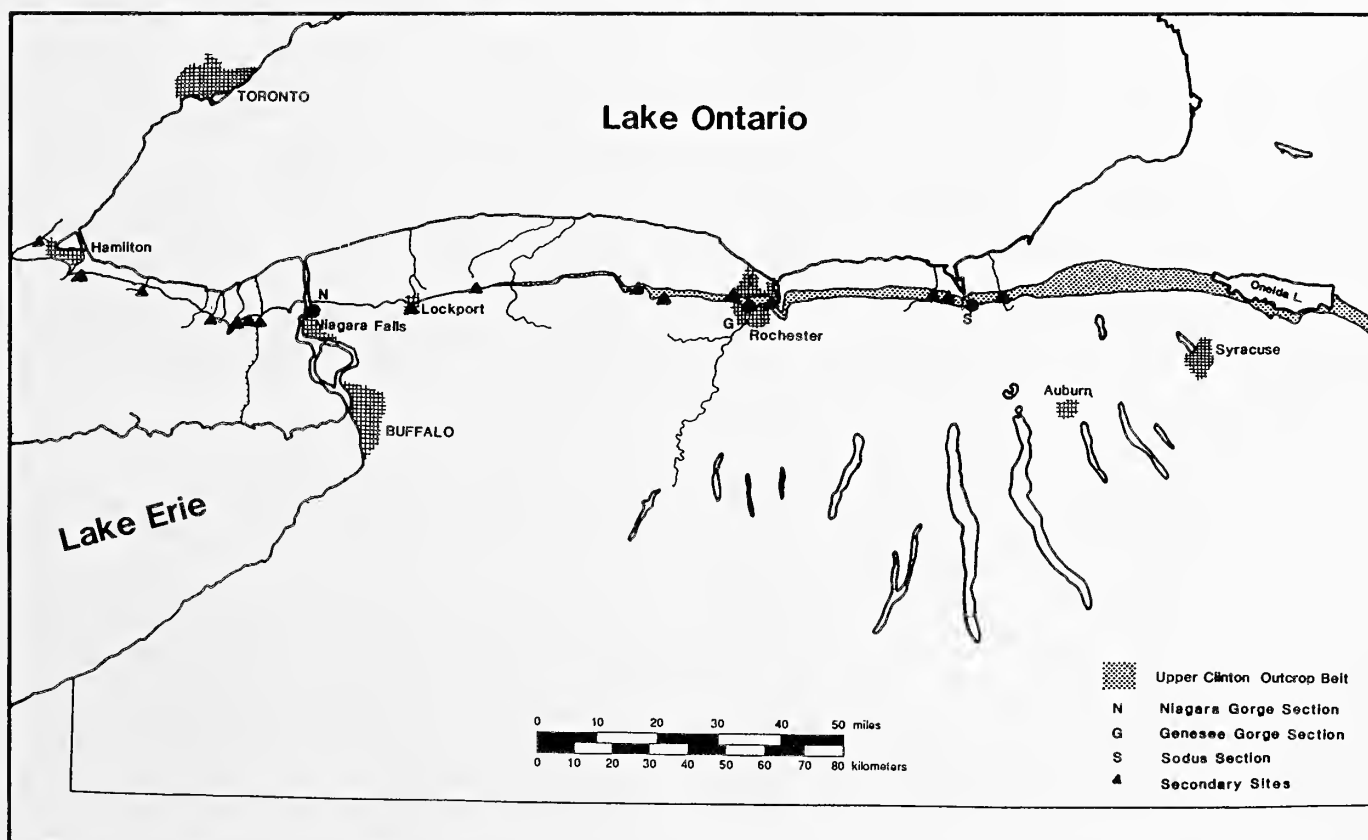


Figure 2. Study area in the Rochester Shale.



Figure 3. Rochester Shale exposure at Niagara Gorge Section, Lewiston, New York. Lower arrow shows top of Irondequoit Limestone; upper arrow shows base of Decew Dolostone.

the faunal spindle diagrams (Figures 4-6). Trilobite distribution is then discussed in this report in terms of a bathymetric gradient established from a study of tempestite proximality (Brett, 1983a) and the brachiopod biofacies defined herein.

Brachiopod biofacies

Western Brachiopod Biofacies 1: *Atrypa*–*Howellella* Biofacies

Definition.—This is the most diverse faunal biofacies of the Rochester Shale. Trepostome and fenestellate bryozoans are the most abundant group. Most of the over eighty bryozoan species described by Bassler (1906) are found exclusively within this biofacies. The dominant brachiopods in this biofacies include *Atrypa* “*reticularis*”, *Howellella crista*, *Leptaena* “*rhomboidalis*”, *Plectatrypa nodostriata*, *Whitfieldella oblata*, *Whitfieldella nitida*, and the ubiquitous genera *Amphistrophia striata*, *Coolinia subplana*, *Resserella elegantula*, and *Stegerhynchus neglectum*. The small brachiopod *Dicoelosia biloba* is common in washings of deeply weathered shale from this biofacies, but is rarely observed in unweathered samples. Other common fossils are the bivalve *Cornellites emaceratus*, the dendroid graptolite *Reticulograptus polymorphus*, the cystoid *Caryocrinites ornatus*, the coronoid *Stephanocrinus angulatus*, and fragments of the crinoid

Crinobrachiatus brachiatus. This biofacies is equivalent to the *Atrypa*–bryozoan patch Association of Brett (1983a).

Occurrence.—The *Atrypa*–*Howellella* Biofacies is best developed in the Lewiston Member (B, D, and E subunits) at the Niagara Gorge section. It is present only in the western half of the outcrop belt; the most easterly appearance of this biofacies is in the northwest Rochester area where a very limited bryozoan community occurs.

This biofacies occurs in moderately fossiliferous to very fossiliferous, medium grey to brownish grey calcareous shales. Interbedded bryozoan biomicrites and biosparites, which vary from lenticular to more continuous beds, occur in these shales.

Taphonomic characteristics.—Storm-event beds represent a significant portion of the rocks deposited within this biofacies, and the full spectrum of storm beds described by Kreisa (1981), Aigner (1985), and Miller et al. (1988) are well-represented. These can vary greatly in structure and fauna from the immediately overlying beds (Figure 7). They include smothered brachiopod beds (generally never more than a few individuals thick); smothered trepostome bryozoan colonies in life position (2 to 10 cm-thick bryozoan boundstone with micrite matrix); and winnowed, fragmented, and corraded bryozoan and brachiopod coquinites (ranging from very thin fossil hash beds to 10 cm-thick biosparites, Figure 8).

Environmental interpretation.—The *Atrypa*–*Howellella* Biofacies represents a shallower-water shelf environment that occurred above maximum storm-wave base but below fair weather wave base (and below storm-wave base for a few weak and/or distant storms), and is the shallowest of the western brachiopod biofacies. Evidence of corrasion on fossil fragments, reworked shell beds, and smothered horizons all suggest that background sedimentation was slow and that deposition was controlled by storms and varied according to their intensity (Brett and Baird, 1986). Very strong storms winnowed the substrate and resulted in the deposition of poorly washed biomicrites to well-washed biosparites composed of fragmented fossil material. Weaker or more distant storms produced winnowing effects farther upslope (presumably north of the present outcrop belt). As a result, suspended muds moved downslope as turbidity or gradient currents that inundated the sea floor by smothering the benthic fauna with a minimal disturbance (see Aigner, 1985; Brett, 1983a; Miller et al., 1988). Storms of intermediate strength produced a complete gradation of event beds between these two extremes. Background sedimentation of lesser importance may perhaps be manifested as a mud matrix deposited within in situ bryozoan colonies by the baffling of muddy currents, but it is indistinguishable from storm blanketing.

Western Brachiopod Biofacies 2: *Striispirifer* Biofacies

Definition.—This biofacies is part of a brachiopod-dominated community, and the most common genus is the spiriferid brachiopod *Striispirifer niagarensis*. *Striispirifer* commonly occurs as patches of very densely packed shell pavements (Figure 9). Other brachiopods commonly found in this community include *Atrypa*, *Leptaena*, *Eospirifer radiatus*, and the ubiquitous genera *Amphistrophia* and *Stegerhynchus*. Other fossils found in this biofacies include dendroid graptolites and the crinoids *Asaphocrinus ornatus* and *Homocrinus parvus*. This biofacies corresponds in all respects to the *Striispirifer* Association of Brett (1983a).

Occurrence.—The *Striispirifer* Biofacies is best developed in the A, upper B, and lower D units of the Lewiston Member in the Niagara Gorge section. These units are located between the poorly fossiliferous dark grey shales characterized by the *Amphistrophia*–*Stegerhynchus*

NIAGARA GORGE

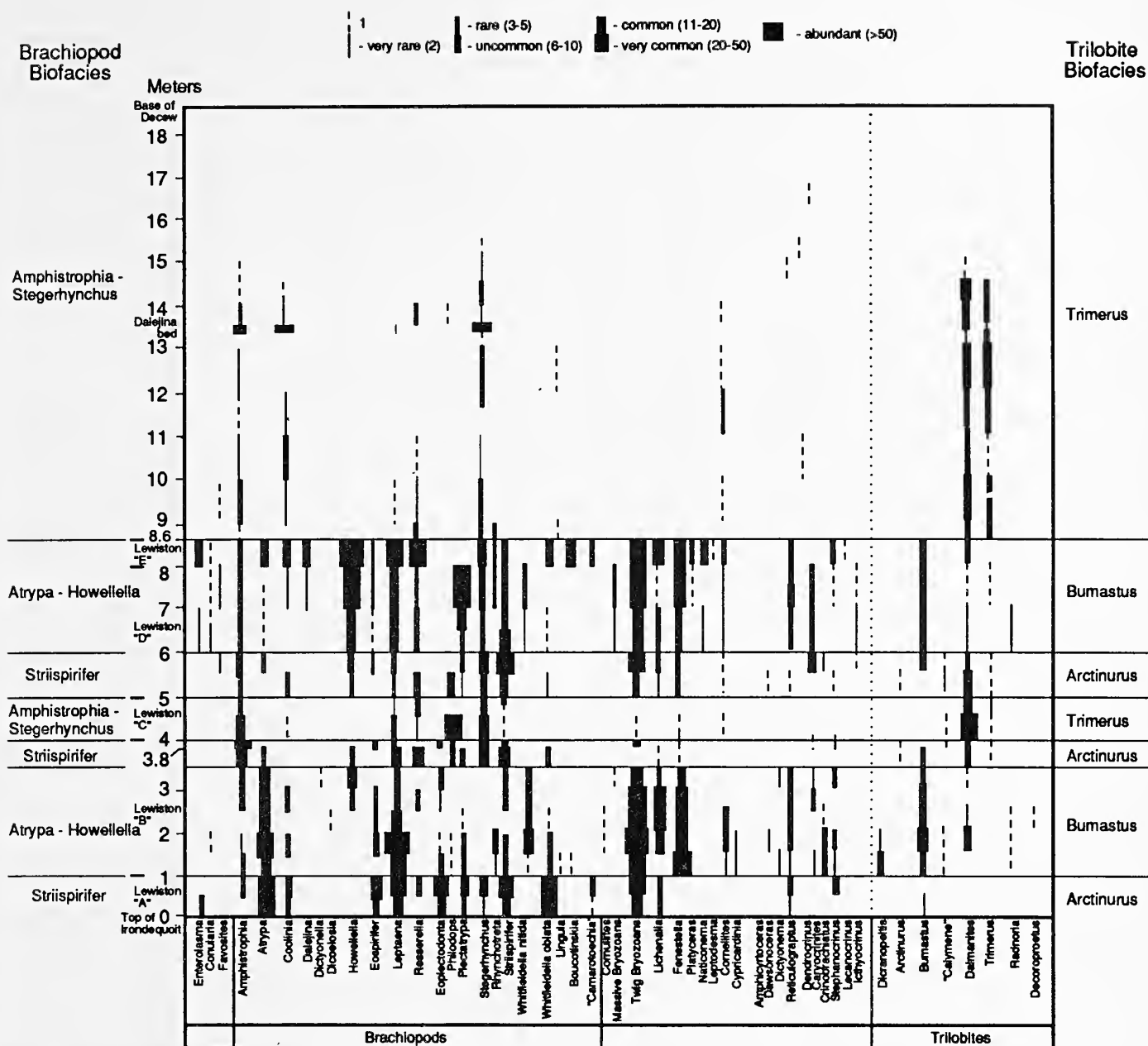


Figure 4. Fauna distribution in the Niagara Gorge section at Lewiston, New York.

Biofacies and the fossiliferous shales and biomicrites with a *Atrypa-Howellella* Biofacies. Found only in the western portion of the outcrop belt, the *Striispirifer* Biofacies is well-exposed in the Niagara and Lockport areas, and good examples have been found in the Brockport area. This biofacies grades into its eastern counterpart, the *Eospirifer-Dalejina* Biofacies, about 25 km to the east in the Rochester area. The lower 1.0 to 4.0 m of the Rochester Shale at Genesee Gorge contains a fauna intermediate between these two biofacies, with both trilobite and brachiopod elements from each found together.

The *Striispirifer* Biofacies occurs within mainly unfossiliferous to

slightly fossiliferous medium grey to brownish grey calcareous shales. Rare 1.0 to 5.0 cm-thick calcisiltites are also present.

Taphonomic characteristics.—Brachiopods are often found in life position (Figure 9) at the bases of unfossiliferous mud layers that average 2–6 cm in thickness. Articulated crinoids complete to the holdfast also are found current-aligned and attached to brachiopods (taphonomic Category I of Meyer et al., 1989). This represents a rapid burial of the sea floor by a storm-generated mud layer. An excellent example of this is the *Homocrinus* interval within the lower Lewiston Member, in which the only known trilobite meraspid (*Decoroproetus*) known from

GENESEE GORGE

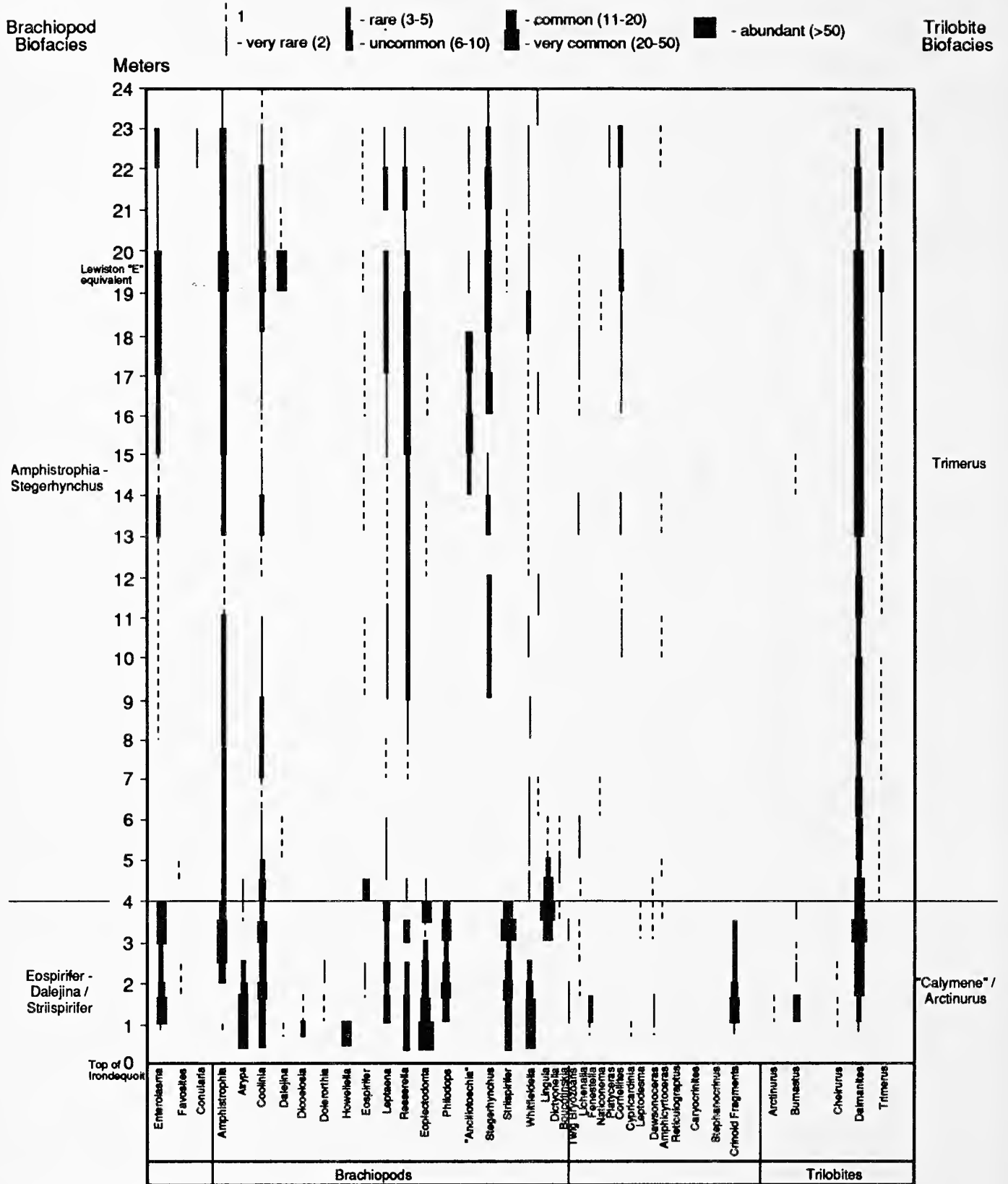


Figure 5. Fauna distribution in the Genesee Gorge section at Rochester, New York.

the Rochester Shale have been found. *Homocrinus parvus* itself is an extremely small crinoid with a delicate, hairlike column and arms. Despite its extremely fragile nature, specimens of *Homocrinus* are found intact in large numbers. Other intervals that consist of thin layers of sparsely distributed, disarticulated, fragmented trilobite, brachiopod, and crinoid material may possibly record either direct disturbance by storm waves that periodically reached to greater depths or, more likely, slow background sediment accumulation.

Environmental interpretation.—The *Striispirifer* Biofacies represents a relatively shallow-water environment near maximum storm-wave base, and is deeper than the *Atrypa-Howellella* Biofacies. Storm waves periodically disturbed the area, but were not strong enough to cause any significant erosion or winnowing effects. Storm-generated

mud layers episodically blanketed the sea floor and smothered the bottom community. The mud deposition prevented the buildup of thick autochthonous shell beds, and the lack of sea floor erosion and winnowing by storm waves prevented development of condensed, allochthonous shell buildups. Mud deposition and lack of shell pavements severely limited the processes described by Kidwell and Jablonski (1983) as taphonomic feedback.

The sediment/water interface was a fairly barren mud bottom with local brachiopod-shell pavements composed mostly of *Striispirifer* (Figure 9).

Eastern and Western Brachiopod Biofacies 3: Amphistrophia-Stegerhynchus Biofacies

SODUS TRIBUTARY

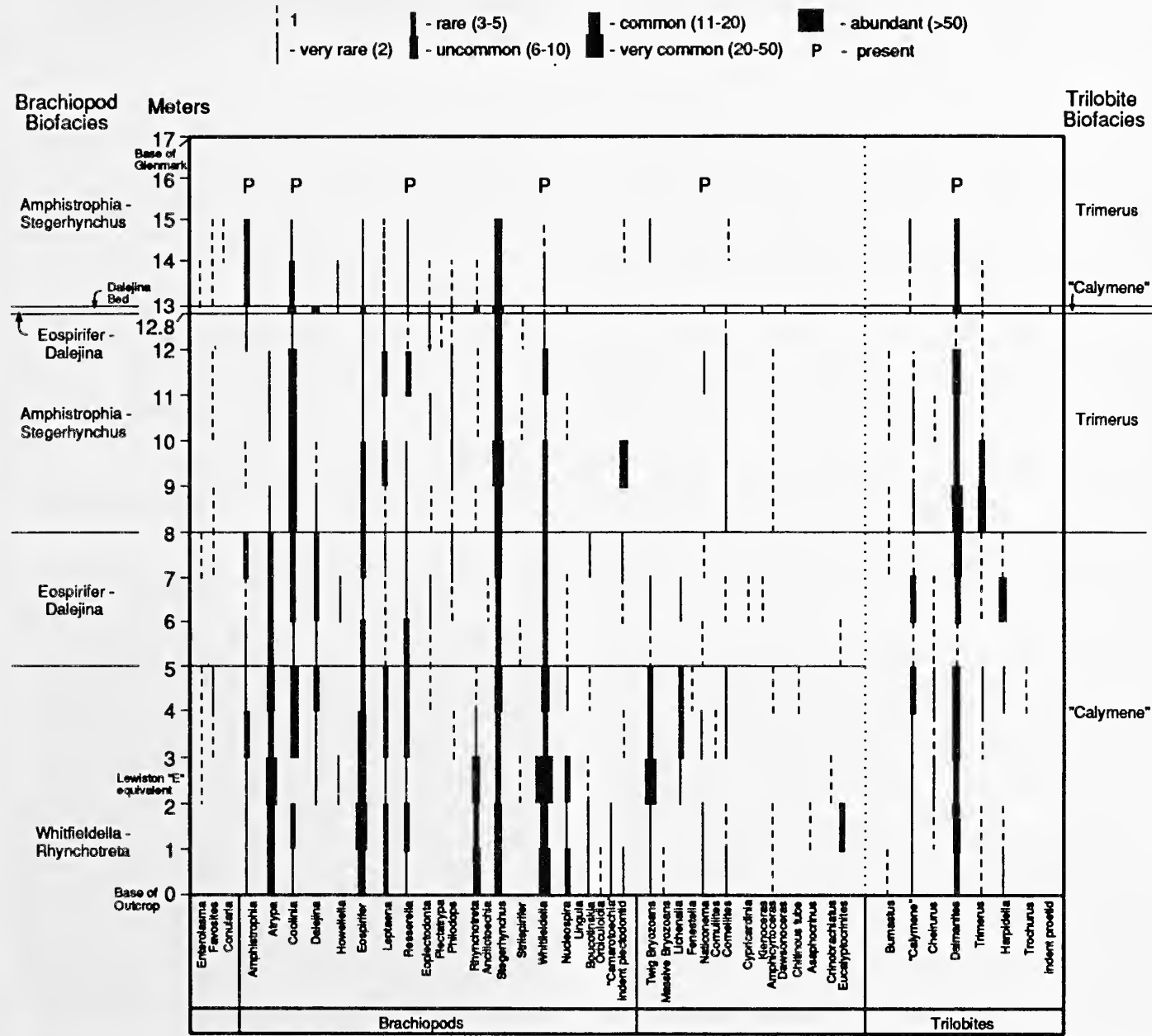


Figure 6. Fauna distribution in the section in an unnamed tributary of Sodus Creek near North Rose, New York.

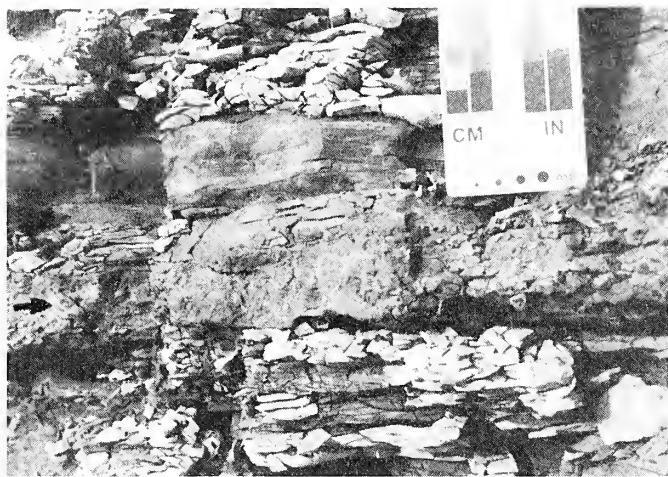


Figure 7. Interbedded bryozoan biomicrite (at arrow), moderately fossiliferous shales, and unfossiliferous calcisiltite, Lewiston "D," Niagara Gorge section, Lewiston, New York.

Definition.—The strophomenid brachiopods *Coolinia subplana* and *Amphistrophia striata* and the small rhynchonellid *Stegerhynchus neglectum* dominate this sparse brachiopod fauna. The small orthid brachiopod *Resserella elegantula* is also often present. Other fossils found in this biofacies include the small rugosan *Enterolasma caliculum* and the bivalve *Cornellites*. This biofacies is equivalent to the *Amphistrophia–Dalmanites* Association of Brett (1983a).

Occurrence.—The *Amphistrophia–Stegerhynchus* Biofacies is the most areally and stratigraphically extensive biofacies in the Rochester Shale, and is present in all the sections that were examined. It is most clearly represented in the Niagara Gorge section, where it makes up all of the Burleigh Hill Member and the medial "C" subunit of the Lewiston Member.

This biofacies is poorly developed in the Sodus area, where strata equivalent to the Burleigh Hill Member (Gates Member) contain a fairly diverse fauna with several brachiopod genera (e.g., *Eospirifer*, *Whitfieldella*) that are more typical of more diverse, shallow-water biofacies. The very poorly exposed Lewiston "C" interval (studied in Wolcott Creek) contains a much more impoverished fauna that is very

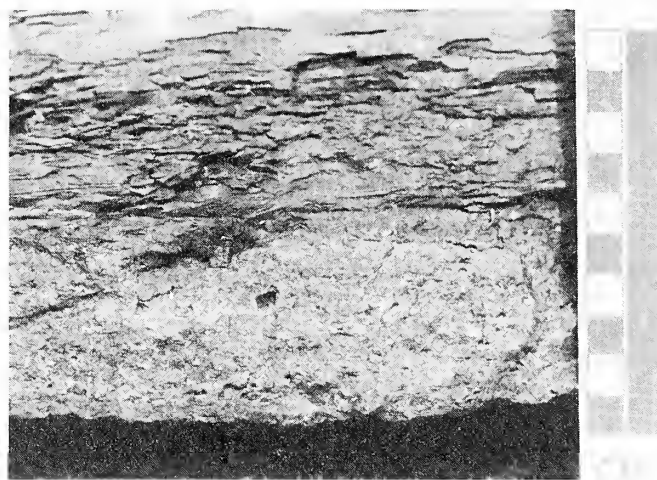


Figure 8. Brachiopod coquinite, top of Lewiston "B," Niagara Gorge section, Lewiston, New York.

similar to the *Amphistrophia–Stegerhynchus* Biofacies at Rochester and Niagara Falls.

Nearly barren, dark grey, fissile to platy, somewhat calcareous shale is the dominant lithology. The upper half of the Burleigh Hill Member consists of lighter grey calcareous or dolomitic shales. Narbonne (1975) reported up to 50% carbonate content at the Burleigh Hill type section. All of the sections also have intervals of varying thickness with 1.0–15 cm-thick calcisiltite beds that are interbedded with the shales. These calcisiltites often show grading, escape burrows, and sole marks. The shales have a typical *Amphistrophia–Stegerhynchus* Biofacies, but the calcisiltites, although commonly bioturbated, usually lack macrofossils.

Taphonomic characteristics.—Fossil material is sparsely distributed throughout this biofacies, and distinct shell beds similar to those observed in the other Rochester Shale biofacies are not present. Bedding surfaces covered with patchily distributed fossil fragments occur uncommonly. Horizons with articulated trilobite carcasses occur very rarely (see *Trimerus* Biofacies).

Environmental interpretation.—The *Amphistrophia–Stegerhynchus* Biofacies represents a deeper water environment below storm-wave



Figure 9. *Striispirifer* shell pavement, top of Lewiston "B," Lockport, New York (x0.5).



Figure 10. Fossil debris bed, unnamed tributary of Sodus Creek, near North Rose, New York (x2.0).

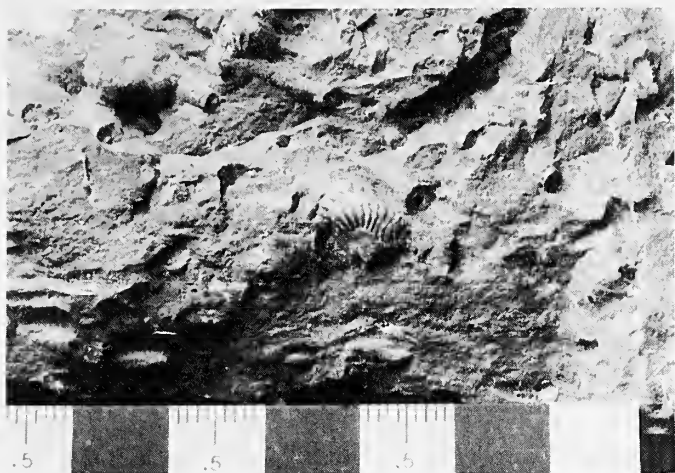


Figure 11. Complete enrolled calymenid (*Sthenarocalymene*?) within brachiopod and bryozoan bed, unnamed tributary of Sodus Creek, near North Rose, New York. Scale in centimeters.

base, and deposition was probably dominated by accumulation of mud and silt tempestites. Living animals were periodically overwhelmed by these mudflows and suffocated. The dead organisms may then have been transported slightly downslope and deposited to produce horizons with articulated individuals.

Eastern Brachiopod Biofacies 1: *Whitfieldella*–*Rhynchotretra* Biofacies

Definition.—The *Whitfieldella*–*Rhynchotretra* Biofacies is the most diverse assemblage of the eastern Rochester Shale. It is somewhat less diverse than its stratigraphic equivalent in the west, the *Atrypa*–*Howellella* Biofacies. The fauna is dominated by a rich brachiopod assemblage that includes *Whitfieldella*, *Atrypa*, *Rhynchotretra*, *Nucleospira*, *Eospirifer*, *Leptaena*, and the ubiquitous genera *Stegerhynchus*, *Coolinia*, and *Amphistrophia*. The foliose bryozoan *Lichenalia* also occurs commonly in this biofacies. Small patches of trepostome bryozoa are rarely present within the Lewiston “E” interval.

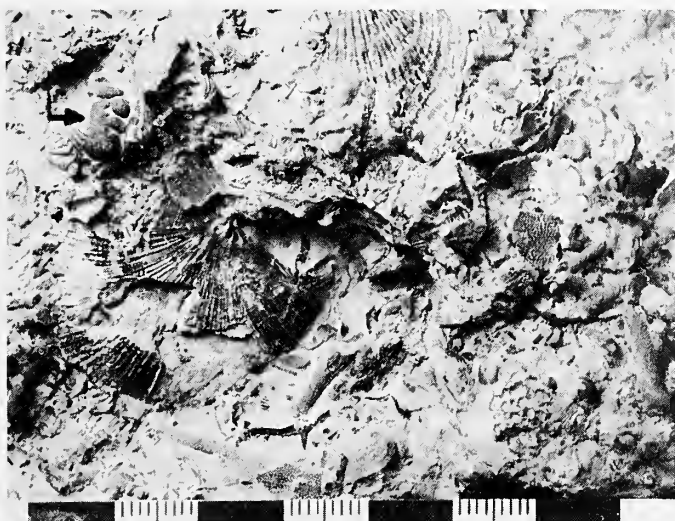


Figure 12. Fragmented brachiopod and trilobite shell bed (calymenid cranium at arrow has ctenostome bryozoan borings), unnamed tributary of Sodus Creek, near North Rose, New York. Scale in centimeters.

Occurrence.—The *Whitfieldella*–*Rhynchotretra* Biofacies occurs in sections in the eastern portion of the study area. These include Wolcott Falls, an unnamed tributary of Sodus Creek, and several other major creeks in the area.

The dominant lithology of this biofacies is a dark grey, slightly calcareous to very calcareous shale that weathers to a medium to dark brown color. Within these beds (stratigraphically equivalent to the Lewiston “E” beds of the west), most of the fossil material is contained within very calcareous mudstone and biomicrite beds. These are 3.0 to 15.0 cm thick and are separated by 10 to 100 cm-thick intervals of fairly unfossiliferous to moderately fossiliferous shales. Several barren calcisiltite beds occur above and below this biofacies and separate these beds from the deeper water beds of the *Eospirifer*–*Dalejina* Biofacies.

Taphonomic characteristics.—The *Whitfieldella*–*Rhynchotretra* Biofacies (Lewiston “E” interval) is very similar to the western *Atrypa*–*Howellella* Biofacies because most of the fossil material occurs within very calcareous beds. In the case of the Eastern Biofacies, these fossiliferous beds are composed mainly of brachiopods (rather than bryozoans), are up to 15 cm thick, and can vary greatly in character. These beds typically show evidence of storm disturbance. Undamaged and articulated brachiopods stacked on one another or mostly fragmentary brachiopod material occur in these beds.

Another type of storm-produced event bed found within this biofacies consists of in situ, smothered-bottom assemblages. One such lenticular bed, approximately 4.0 to 7.0 cm thick and almost 2.0 m in diameter, is composed of a patch of large, fragile, foliose *Lichenalia* bryozoan colonies. These occur within a very calcareous mudstone and contain several dozen complete *Eucalyptocrinites* individuals and large unbroken *Eridotrypa* specimens. One of the latter has a *Boucotinskia* brachiopod preserved in living position. Above this bed are the typical poorly fossiliferous shales that make up most of the section.

Environmental interpretation.—The *Whitfieldella*–*Rhynchotretra* Biofacies represents a shallow-water environment above storm-wave base but below fair weather wave base, and is the shallowest of the Eastern Brachiopod Biofacies. Storms of varying intensity and proximity to the site of deposition produced a spectrum of event beds, similar to the laterally equivalent western sequence that contains the *Atrypa*–*Howellella* Biofacies. Smothered bottom assemblages, slightly disturbed in situ shell beds, strongly disturbed brachiopod and trilobite hash beds, barren calcisiltites, and barren to poorly fossiliferous mudstone (shale) tempestites are all represented. Most of the sedimentation probably occurred during storm depositional events. Background sedimentation, if any, is probably represented by the mud between bryozoan plates and branches and by the thin mud layers with scattered brachiopod and trilobite fragments that sometimes occur between shell beds and barren shale intervals. Calcisiltite beds were deposited just above storm-wave base where silt-sized carbonate material could settle out.

Eastern Brachiopod Biofacies 2: *Eospirifer*–*Dalejina* Biofacies

Definition.—The *Eospirifer*–*Dalejina* Biofacies of the eastern Rochester Shale consists of a fairly diverse brachiopod-dominated assemblage. The more common genera include *Atrypa*, *Eospirifer*, *Whitfieldella*, *Dalejina hybrida*, *Eoplectodonta transversalis*, and the ubiquitous genera *Stegerhynchus*, *Coolinia*, and *Amphistrophia*.

Occurrence.—The *Eospirifer*–*Dalejina* Biofacies is found in sections in the eastern portion of the study area. These include Wolcott Falls, an unnamed tributary of Sodus Creek, and several other major creeks in the area.

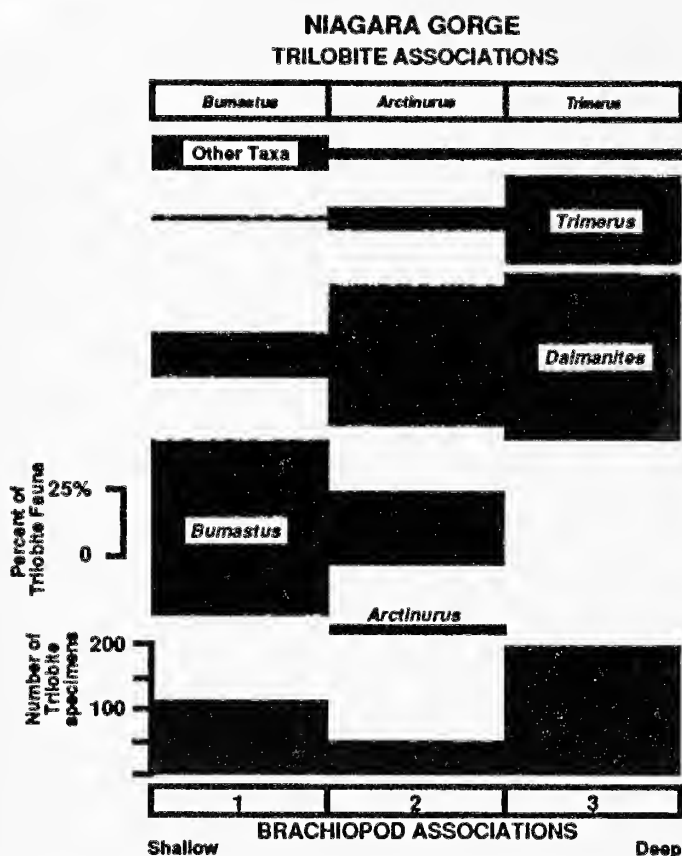


Figure 13. Western Rochester Shale brachiopod distribution. Numbered (1-3) brachiopod associations include the following brachiopod biofacies: 1. *Atrypa-Howellella*; 2. *Striispirifer*; 3. *Amphistrophia-Stegerhynchus*.

The brachiopod fauna within the lower 5.0 m of the Rochester Shale at the Genesee Gorge in Rochester represents a gradation between the eastern *Eospirifer-Dalejina* Biofacies and the western *Striispirifer* Biofacies, and contains elements of both. At Brockport (27 km farther west), this mixed fauna is completely replaced by the *Striispirifer* Biofacies.

The *Eospirifer-Dalejina* Biofacies occurs within a dark grey, poorly to slightly fossiliferous, slightly calcareous siliciclastic mudstone. Rare barren calcisiltites, thin shell beds, and fossil hash beds are intercalated with these more barren mud packages. The *Eospirifer-Dalejina* Biofacies grades up-section into the *Amphistrophia-Stegerhynchus* Biofacies.

The fauna of the *Eospirifer-Dalejina* Biofacies recurs 4.2 m below the top of the formation within the "*Dalejina* Bed" (Figure 6). This thin but very widespread interval varies in nature from a fossil hash layer only a few millimeters thick up to a 5.0 cm-thick limestone bed, and sometimes consists of an amalgamation of several thin shell beds. The *Dalejina* Bed often shows these extremes within a few meters of lateral distance. It can be traced within the Gates and Burleigh Hill Members from Wolcott, New York, to Grimsby, Ontario, a distance of 230 km.

Taphonomic characteristics.—The *Eospirifer-Dalejina* Biofacies contains thin shell beds less than 2 cm thick and fossil debris layers (Figure 10) that indicate that storm waves periodically disturbed the sea bottom. These events are, however, much rarer and apparently far weaker in effect than in the *Whitfieldella-Rhynchotrete* Biofacies (Lewiston "E" interval). The concept of tempestite proximality (Aigner,

1985; Brett et al., 1986; Norris, 1986; Miller et al., 1988) suggests that the *Eospirifer-Dalejina* Biofacies was deposited in deeper water.

Environmental interpretation.—The *Eospirifer-Dalejina* Biofacies represents a depositional regime near storm-wave base that is slightly deeper than the *Whitfieldella-Rhynchotrete* Biofacies. Disturbance by storms occurred periodically, but their direct effect was not as strong as that within the shallower portions of this section. This resulted in decreased shell-bed development. Storms accounted for much sediment transport and accumulation. These storms are represented by poorly fossiliferous packages of mudstone that were deposited as storm-generated turbidity flows or gradient currents.

Trilobite biofacies

Previous studies

Little work has been done on Silurian trilobite biofacies. Mikulic (1981) reviewed the overall distribution of trilobite faunas within Paleozoic carbonate buildups, with an emphasis on North American occurrences. Most other studies have concentrated on European, particularly British, occurrences. Thomas (1979, Fig. 2 and 3) plotted trilobite distribution in the context of onshore to offshore lithofacies belts and grouped trilobites into five facies-controlled associations. These include the sandstone belt *Acaste-Trimerus* Association, the shelf limestone *Proetus-Warburgella* Association, the shale belt *Dalmanites-Raphiophorus* Association, the sparry algal limestone *Radnor-Cornuproetus* Association, and the graptolitic shale *Delops-Miraspis* Association. Of these, the shale belt facies is most similar to the Rochester Shale lithology, although all these facies can be found among the other Silurian units within New York State (see Gillette, 1947, for examples). Many of the British trilobite genera also occur in New York and Ontario.

Mikulic and Watkins (1981) made a more detailed study of trilobite distribution within the Ludlovian Series in the Welsh borderland. They plotted trilobite distribution against a depth gradient, using facies change as a depth indicator, and found a distribution pattern similar to Thomas' (1979) sandstone to shale belt pattern from the Wenlockian.

Mannil (1982a, 1982b) demonstrated that trilobite biofacies in the east Baltic region were also very similar to those reported from Britain, with encrinurids and proetids dominating the shallower, generally carbonate-rich facies, and calymenids and *Dalmanites* in the deeper, generally mudstone facies.

Chlupáč (1987) described eighteen diverse trilobite assemblages from the Silurian of central Bohemia. These rocks were deposited in an area of frequent volcanic activity. Trilobite-bearing lithologies range from shallow-water carbonates to deeper-water shales, all with varying amounts of volcanoclastic material.

Most recently, Ludvigsen and Tripp (1990) described three trilobite associations from the Yukon Territory: an *Otarion* Association within dark grey, highly argillaceous lime mudstones, a *Stenopareia* Association from an off-white crystalline biosparite, and a *Hedstroemia* Association from a debris flow derived from the side of a carbonate bank. These three associations are examples of the illaenid and proetid dominance that is so common in Silurian shallow shelf carbonates.

Bumastus Biofacies

Definition.—The *Bumastus* Biofacies is characterized by dominance of the small illaenid *Bumastus ioxus*. This species composes approximately 50-90% of the trilobite fauna within any one sample (mean of

65%). The ubiquitous dalmanitid *Dalmanites limulurus* is ranked second in abundance, and makes up 5-30% of the trilobite fauna in this biofacies (mean of 15%). Other trilobites present, in decreasing abundance, are *Sthenarocalymene?* sp., *Dicranopeltis nereus*, and *Radnorina* sp.; each of these may compose up to 10% of the trilobite material within any sample. *Trimerus delphinocephalus*, *Arctinurus boltoni*, and *Decoroproetus corycoeus* are found very rarely, and are most often found within the less-diverse assemblages of this biofacies. *Deiphon pisum* occurs within this biofacies in the north Rochester area.

Occurrence.—The *Bumastus* Biofacies is associated with the western brachiopod *Atrypa-Howellella* Biofacies. It is best developed in the Lewiston Member (B, D, and E subunits) at the Niagara Gorge section.

Taphonomic characteristics.—Trilobite material within the smothered horizons (see *Atrypa-Howellella* Biofacies) often shows very little, if any, disturbance or transport. Molt assemblages and carcasses are often found articulated. A possible cluster of molt ensembles (sensu Speyer and Brett, 1985) was also found (Tetreault, 1990). Other evidence for rapid burial includes brachiopods in living position and complete crinoids and cystoids still attached by their holdfasts to brachiopods and bryozoans.

Fossil material within the bryozoan and brachiopod biomicrites and mudstones is normally very well-preserved with little, if any, fragmentation. Trilobite material is usually disarticulated, although articulated brachiopods and complete cystoid calyces are common.

The bryozoan and brachiopod biosparites with the *Bumastus* Biofacies normally have highly fragmented fossil material. The fragmentation is sometimes so complete that even the most distinctive brachiopods cannot be identified (Figure 8). Trilobite material is similarly fragmented. Within these beds, the very thick, characteristically pitted cuticle of large *Trimerus* individuals and the schizochroal eye of *Dalmanites* are often the only trilobite fragments that can be identified with any certainty.

Trilobite traces are rare in this biofacies, although at least two genera of trilobites (*Dalmanites* and *Trimerus*), and possibly more, were capable of producing excavations (Osgood and Drennen, 1975; Tetreault, 1990). Rare specimens of *Rusophycus*, possibly attributable to *Trimerus*, are found on the bases of skeletal grainstones within the Lewiston "E" submember. This indicates that this trilobite burrowing behavior also occurred in this environment and not exclusively in the deeper environment where *Rusophycus* is common (see *Trimerus* Biofacies). This type of activity is therefore not habitat-specific. The frequency of storm winnowing of the substrate in a relatively proximal environment, combined with the activities of an active infauna (bioturbation), probably severely reduced the preservation potential of trilobite trace fossils. The cohesiveness of the substrate may also have been less in this shallower, higher-energy environment than in the deeper environments.

Arctinurus Biofacies

Definition.—The *Arctinurus* Biofacies is characterized by a moderately diverse trilobite fauna dominated by the ubiquitous *Dalmanites limulurus*, which constitutes approximately 75% of the fauna. The remaining genera occur in relatively equal proportions, with variations between outcrops and horizons. However, the most characteristic trilobite of this second grouping is the large lichid *Arctinurus boltoni*, which is confined to this biofacies. Other trilobites include *Trimerus delphinocephalus*, the proetids *Decoroproetus corycoeus* and *Radnorina* sp. (the latter occurring more commonly in the *Bumastus-Dalmanites* Biofacies), a calymenid (*Sthenarocalymene?*), and the illaenid genera *Illaeonoides* (previously unreported) and *Bumastus*. The lichid

Trochurus halli occurs very rarely.

Occurrence.—The *Arctinurus* Biofacies occurs with the western *Striispirifer* Biofacies. The biofacies is especially well-developed in the Niagara and Lockport areas.

Taphonomic characteristics.—The trilobite material found in this biofacies is normally well-preserved. There is less breakage of skeletal elements (e.g., complete cephalon or pygidia) than in the presumably shallower-water *Bumastus* Biofacies, which occurred in a higher-energy environment.

Articulated carcasses and molt ensembles are normally found at the bases of unbedded, unfossiliferous mud layers. These average 2-6 cm in thickness, and are mud tempestites with brachiopods and articulated crinoids often in living position.

Trimerus Biofacies

Definition.—This is the only biofacies of the Rochester Shale in which trilobite material is often the numerically dominant body fossil element. It sometimes constitutes up to 75% of the fossil material (Niagara section, Burleigh Hill Member), although figures in the range of 15-50% are more characteristic. Of the two trilobites found within this biofacies, *Dalmanites limulurus* is by far the most common, and generally makes up 60-95% of the trilobite skeletal elements within any one sample (mean of 65%). *Trimerus delphinocephalus* composes the remaining fraction. A calymenid (*Sthenarocalymene?*) is also found rarely in the Burleigh Hill Member in the eastern outcrops.

Occurrence.—The *Trimerus* Biofacies occurs with the areally extensive *Amphistrophia-Stegerhynchus* Biofacies. This trilobite biofacies can be found throughout the outcrop belt.

Taphonomic characteristics.—Most trilobite material is disarticulated, and complete specimens are extremely rare. At the Gates Barge Canal near Rochester, however, complete specimens of *Dalmanites* can be found with some regularity. These trilobites occur in several beds that represent carbonate-siliciclastic mud tempestites that are exposed within the Lewiston Member and are 21.5 and 22.5 m below the top of the Rochester Shale. These horizons are quarried by local collectors, who have recovered well over one hundred complete *Dalmanites* specimens from the base of these beds. More than 95% of these specimens are dorsal-side down and oriented with the cephalon pointed north-northeast. These individuals were almost certainly swept up by storm-generated currents, smothered, and carried a short distance before the carcasses settled out of the mud slurry. The shape of their exoskeleton and protruding appendages may have resulted in a tendency to settle dorsal-side down, much like a shuttlecock, oriented NNE by the slowing mud slurry. Simultaneous burial would have prevented any reorientation by currents. Allison (1986) experimentally demonstrated the durable nature of freshly killed marine arthropods. His study suggests that the trilobite carcasses could easily have been transported a short distance without any damage to the dorsal shield. The excellent preservation of these trilobites probably results from almost simultaneous death and burial.

Among the disarticulated trilobite material, *Dalmanites* cephalon are much rarer than pygidia (Tetreault, 1990). This may result from the cephalon's more fragile nature. Speyer (1987) reported similar observations on the disarticulated remains of the morphologically analogous Middle Devonian asteropygid *Greenops boothi*. The equally sturdy cephalon and pygidia of *Trimerus* are found in nearly equal numbers.

"Calymene" Biofacies

Definition.—The "Calymene" Biofacies is dominated by the ubiquitous *Dalmanites limulurus*, which makes up 20-75% of the trilobite

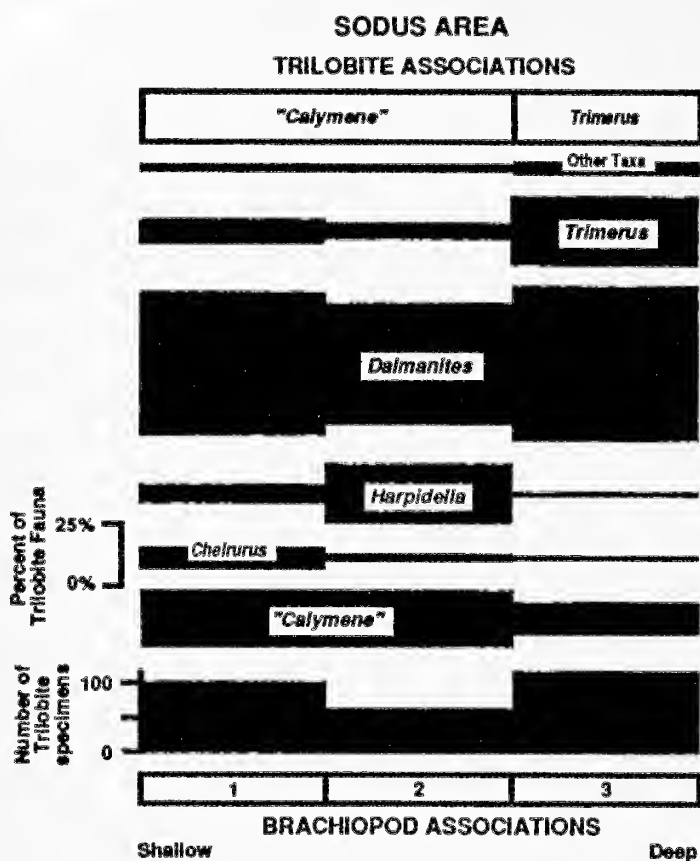


Figure 14. Eastern Rochester Shale trilobite distribution. Numbered (1-3) brachiopod Associations include the following brachiopod Biofacies: 1. *Whitfieldella-Rhynchotreta*; 2. *Eospirifer-Dalejina*; 3. *Amphistrophia-Stegerhynchus*.

cephala and pygidia within individual samples (mean of 50%). "Calymene" (*Sthenarocalymene*?) is common (10-30%, mean of 20%), particularly within the brachiopod shell-beds and bryozoan-bearing beds. Slightly less common is the proetid *Harpidella* (0-40%, mean of 13%); this genus was previously unknown from the Rochester Shale and occurs more commonly within the beds that are transitional with the *Trimerus* Biofacies. *Harpidella* is found only in the eastern part of the outcrop belt and has not been found farther west than Spencerport, New York. *Cheirurus niagarensis* is a rare element in this biofacies (0-20%, mean of 6%) and is more common within the shallower bryozoan and brachiopod shell-beds. Virtually restricted to the eastern portion of the study area, *Cheirurus* is generally found no farther west than the Genesee Gorge section at Rochester (the exceptions being a cranidium found at Stoney Creek, Ontario, and a pygidium at 16 Mile Creek, Ontario). Other rarely occurring trilobites (in decreasing order of importance) include *Trimerus delphinocephalus* (mean of 8%), *Trochurus halli*, and *Bumastus* sp.

Occurrence.—The "Calymene" Biofacies is found both with the *Whitfieldella-Rhynchotreta* Biofacies and with the *Eospirifer-Dalejina* Biofacies.

Taphonomic characteristics.—Storm beds that are composed of undamaged and articulated brachiopods stacked on top of one another sometimes contain complete, articulated calymenids in various positions (Figure 11). These latter specimens probably represent individuals killed during storm events. Most specimens are in an outstretched posi-

tion, with a small number being enrolled. A similar pattern was found by Brandt-Velbel (1985) in *Flexicalymene* from the Cincinnati shales (Upper Ordovician) of southwest Ohio. Disarticulated trilobite material is often oblique to bedding, and usually unbroken and unabraded. This suggests that, although there may have been disturbance, transport was probably minimal. Storm beds that consist of mostly fragmented fossil material often have trilobite material that shows breakage, abrasion, boring (usually by ctenostome bryozoans), and corrosion (Figure 12). This would indicate that skeletal material sometimes remained at the sediment-water interface for extended periods of time as a consequence of slow background sedimentation, and was often reworked by storms before final burial (Brett and Baird, 1986). Trilobite skeletal elements within the fossil debris layers in the parts of the "Calymene" Biofacies associated with the *Eospirifer-Dalejina* Biofacies are generally unbroken and unabraded.

Trilobite distribution patterns

The most obvious pattern in the Rochester Shale at many outcrops is the symmetrical distribution of species (and therefore of biofacies). This is evident in the Lewiston Member at the Niagara Gorge (Figure 4). The vertical sequence of biofacies includes, from bottom to top of section, the *Bumastus*, *Arctinurus*, *Trimerus*, *Arctinurus*, and *Bumastus* Biofacies. Tempestite proximity, as described by Kreisa (1981), Aigner (1985), and Miller et al. (1988), can be used as a relative depth indicator. By means of storm-event beds within the Rochester Shale, it can be demonstrated that this pattern represents a transgressive-regressive cycle (see Brett, 1982, 1983a, 1983b, and biofacies descriptions herein). The *Bumastus* Biofacies is found associated with shallow-water, proximal-type storm beds (grainstones, graded calcisiltites), and the *Trimerus* Biofacies occurs only with deeper-water, distal-type storm beds (fine-grained calcisiltites and blanketing mudstones). The vertical changes within the section most likely are a direct result of the northern, then southern tracking of mud-bottom communities existing on the gently south-dipping ramp that bordered the Algonquin Arch (Brett, 1983a). Each of the Rochester brachiopod and trilobite biofacies (Figures 13 and 14), from shallowest to deepest, migrated across the outcrop area as the belts tracked their corresponding water depth range.

When the three major sections (Niagara Gorge, Genesee Gorge, and Sodus Tributary) are compared, an east-west pattern becomes apparent (Figures 13-16). The deeper water *Trimerus* Biofacies occurs throughout the study region, but the shallower biofacies change in an east-west direction (Figure 14). In the Rochester area, most of the section is referable to the *Amphistrophia-Stegerhynchus* brachiopod Biofacies and *Trimerus* Biofacies; it is composed of darker, thinly bedded shales that contain very few proximal storm beds. This suggests that it may have been near the basin center. To the west of this area, the *Bumastus* Biofacies occupies the shallowest position, but it is replaced in shallow portions of the eastern side of the basin by the "Calymene" Biofacies. The *Arctinurus* Biofacies of the western sections also grades into the deeper portions of the "Calymene" Biofacies to the east. Both of these changes occur in the Rochester area. Differences in sedimentation offer a possible explanation for this faunal replacement. The east side of the basin (Sodus Bay area) was closer to the clastic sediment source (the Taconian uplands) and therefore received a higher siliciclastic input. Turbidity may therefore have been higher. To the west, farther away from the clastic sediment source, overall turbidity may have been

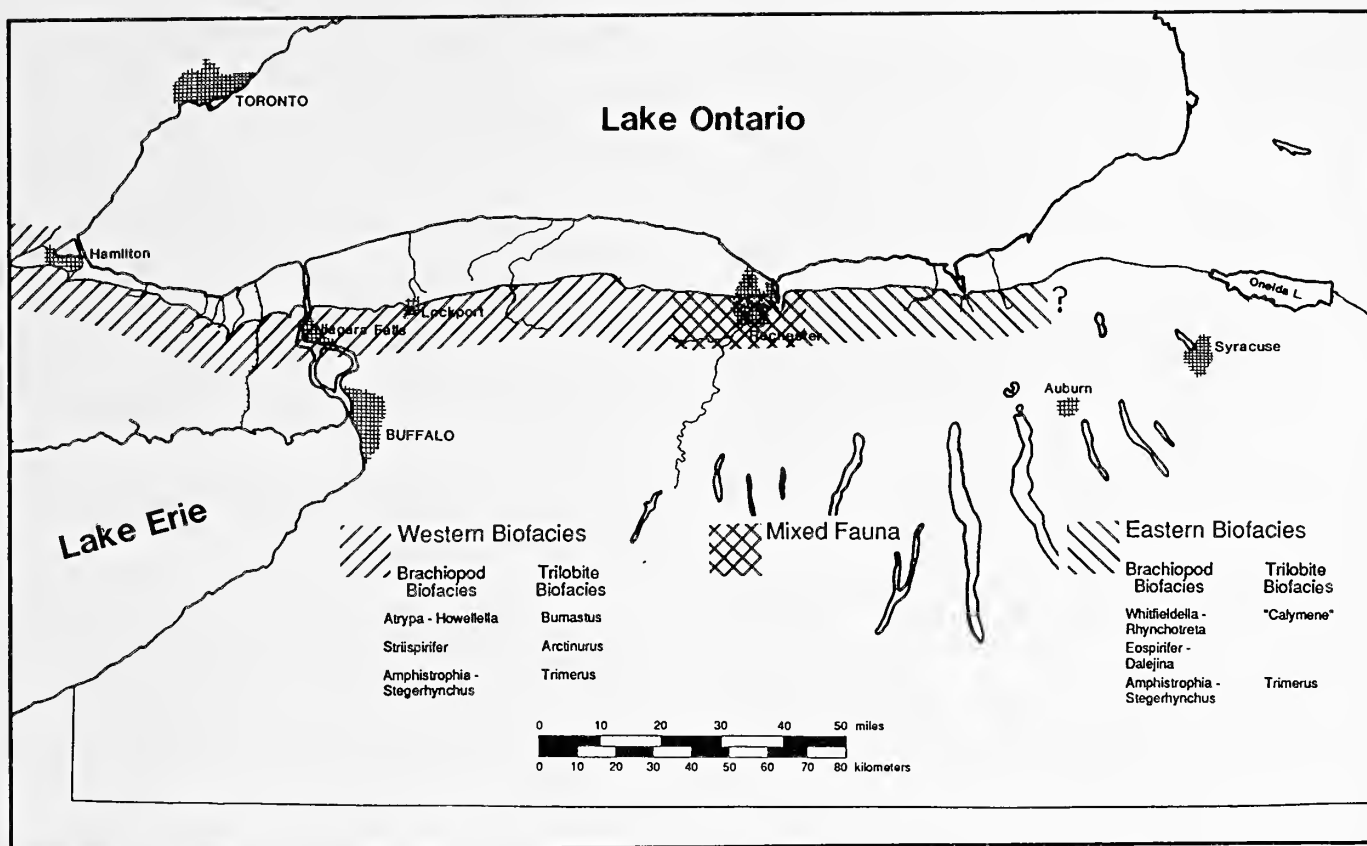


Figure 15. Geographic distribution of Rochester Shale biofacies.

lower. Speyer and Brett (1988) found a similar east-west faunal replacement of Middle Devonian trilobite biofacies over roughly the same region of the Appalachian Basin.

Several larger-scale patterns quickly become evident when the entire trilobite distribution within the Rochester Shale is examined. In contrast to the Ludlovian Series of the Welsh borderland (Mikulic and Watkins, 1981), in which highest trilobite diversity occurred in deeper water, the highest diversity trilobite faunas of the Rochester Shale occurred in the shallower-water, storm-influenced environments. The lower-diversity fauna described by Mikulic and Watkins (1981) in the shallowest biofacies of the Welsh borderland corresponds to a part of the section with the smallest sample sizes. However, the small number of trilobite fragments found in Wales may be a reflection of a true decrease in the importance of the trilobite fraction of the community and a decrease in overall community, population size and diversity in the shallow biofacies (see Mikulic and Watkins, 1981, Figs. 4, 5).

These contrasting patterns between the lower part of the Rochester Shale and the Ludlovian of Wales may reflect the difference in sediment size and accumulation rate within the shallowest environments. Although the shallow-water areas of the Rochester Sea were clear enough to support high-diversity bryozoan biostromes, the higher rates of siliciclastic sedimentation in the Welsh borderland prevented development of a diverse epifaunal community. By this interpretation, lower diversity would be related to higher siliciclastic input, as suggested by Mikulic and Watkins (1981), rather than to depth. At all sections in the upper Burleigh Hill Member of the Rochester Shale, the number and thickness of carbonate silt and mud tempestites increase. Sediment

ROCHESTER TRILOBITE ASSOCIATIONS

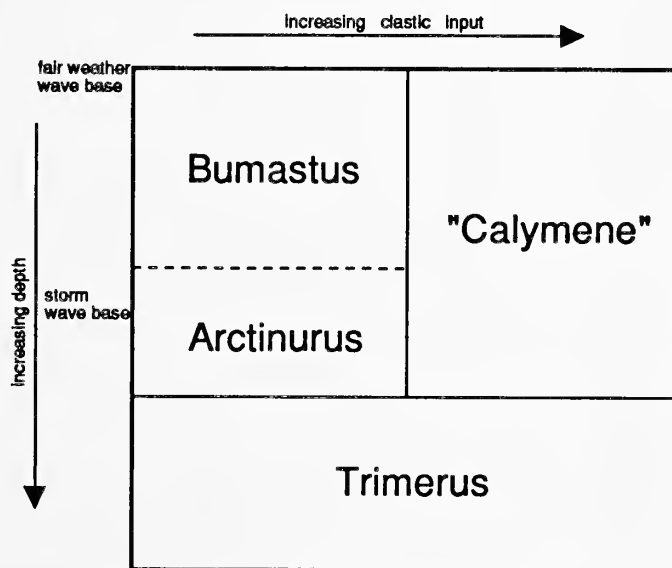


Figure 16. Summary of Rochester Shale trilobite biofacies.

accumulation rates may have been higher than in the lower part of the Rochester Shale; this provides a possible explanation for the low-diversity *Trimerus* Biofacies that dominated during the entire regression into the Decew Member of the Lockport Formation. As in the Welsh borderland, but unlike the Lewiston Member of the Rochester Shale, absolute abundance of trilobite specimens within the uppermost Burleigh Hill Member also decreases towards the top of the section with decreasing water depth. This may be a result of the same environmental conditions, which include increasing sediment accumulation rate, observed within the shallowest Welsh sequence.

The importance of the aulacopleurid *Harpidella* in the "*Calymene*" Biofacies is worthy of note (Figure 14). Although aulacopleurids are typically rare in other Silurian trilobite biofacies, Ludvigsen and Tripp (1990) described an aulacopleurid-dominated *Otarion* Association from dark grey, highly argillaceous lime mudstone of the Yukon Territory. This latter faunal and lithologic association is reminiscent of the Rochester Shale. However, Ludvigsen and Tripp (1990) proposed a deep-water setting for this association that is dissimilar from that of the Rochester Shale.

In earlier studies, shale basins have been thought to be relatively uniform and uninteresting. The division of the Rochester Shale into several sedimentation- and depth-controlled trilobite biofacies illustrates that stratigraphic units of a superficially homogeneous lithology may be characterized by relatively complex paleoecologic patterns.

Acknowledgments

I would like to thank my advisors, C.E. Brett and S.R. Westrop, for their invaluable aid during the M.Sc. project, of which this study was a part. G. Kloc, J. Eckert, and K. Smith graciously loaned material from their private collections. Access was provided to institutional collections by E. Landing, New York State Museum; D. Rudkin and J. Waddington, Royal Ontario Museum; and R. Laub, Buffalo Museum of Science. Photographic facilities were provided by S.R. Westrop at Brock University. Field expenses were partially funded by a Sigma Xi Grant-in-Aid of Research. M. Lozon redrafted Figures 1 and 4-6. J. Tetreault, J. Eckert, R. Esch, and S. LoDuca provided assistance in the field. R. Ludvigsen and S.E. Speyer kindly reviewed this paper and provided many useful comments.

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Redescription of *Glyptoconularia gracilis* (Hall), an Ordovician conulariid from North America

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Abstract

Glyptoconularia gracilis (Hall), currently known from Middle and Upper Ordovician strata of North America, is redescribed and refigured. Ruedemann (1896a, 1896b, 1897) thought that exceptionally preserved specimens of this conulariid are locally abundant in the Utica Shale (upper Middle Ordovician) of New York. However, only one of the nearly one hundred specimens figured by Ruedemann is a *Glyptoconularia*.

Introduction

Glyptoconularia gracilis (Hall) is a rare and highly distinctive conulariid currently known from Middle and Upper Ordovician strata of North America. It is the type and only recognized species of its genus, which was erected by Sinclair (1948, 1952). *Glyptoconularia gracilis* differs from other conulariids in possessing numerous small, straight or aperturally arching transverse corrugations arranged in longitudinal files on the faces. Ruedemann (1896a, 1896b, 1897) illustrated nearly one hundred specimens that he identified as *Conularia gracilis* Hall (= *G. gracilis* (Hall)) from the Utica Shale (upper Middle Ordovician) of New York. Many of these specimens are depicted with well-preserved apertural lappets and/or a basal holdfast. However, subsequent examination of Ruedemann's material (e.g., Ruedemann, 1916; Feldmann et al., 1986) suggests that most of his specimens, including those illustrated as having apertural lappets and a basal holdfast, are not conulariids.

In spite of its unusual facial ornament and uncertainty surrounding the identity of Ruedemann's Utica Shale material, *Glyptoconularia gracilis* has received inadequate attention in the literature on conulariid anatomy and systematics. Previously published descriptions of this species (Hall, 1847; Ruedemann, 1896a, 1896b, 1897; Sinclair, 1952; Moore and Harrington, 1956) omit important anatomical details. Some of these details were covered by Sinclair (1948) in an extended description in his dissertation, but this work has not been published. In the chapter on conulariids in the *Treatise on Invertebrate Paleontology* (Moore and Harrington, 1956), the genus *Glyptoconularia* is listed as a junior synonym of *Sphenothallus* Hall, a taxon that was once widely interpreted as a conulariid (e.g., Moore and Harrington, 1956) but has been removed recently from the group (e.g., Mason and Yochelson, 1985; Feldmann et al., 1986).

The redescription of *Glyptoconularia gracilis* in this report is in general agreement with Sinclair's (1948) unpublished account, but cov-

ers additional anatomical details not noted by previous authors. It is based on examination of seven specimens, most of which are highly fragmentary. The specimens are housed in the following institutions: American Museum of Natural History, New York City (AMNH); Geological Survey of Canada, Ottawa (GSC); New York State Museum, Albany (NYSM); State University of Iowa, Iowa City (SUI); and University of Minnesota, Minneapolis (UMPC).

Systematic paleontology

Phylum CNIDARIA Hatschek, 1888

Order CONULARIIDA Miller and Gurley, 1896

Genus GLYPTOCONULARIA Sinclair, 1952

GLYPTOCONULARIA GRACILIS (Hall, 1847)

Plate 1, figures A-E

Conularia gracile Hall, 1847, p. 224, Pl. 59, figs. 7a, b.

Conularia gracilis Hall. RUEDEMANN, 1896a, Pl. 9, figs. 5-6; RUEDEMANN, 1897, Pl. 2, figs. 5-6.

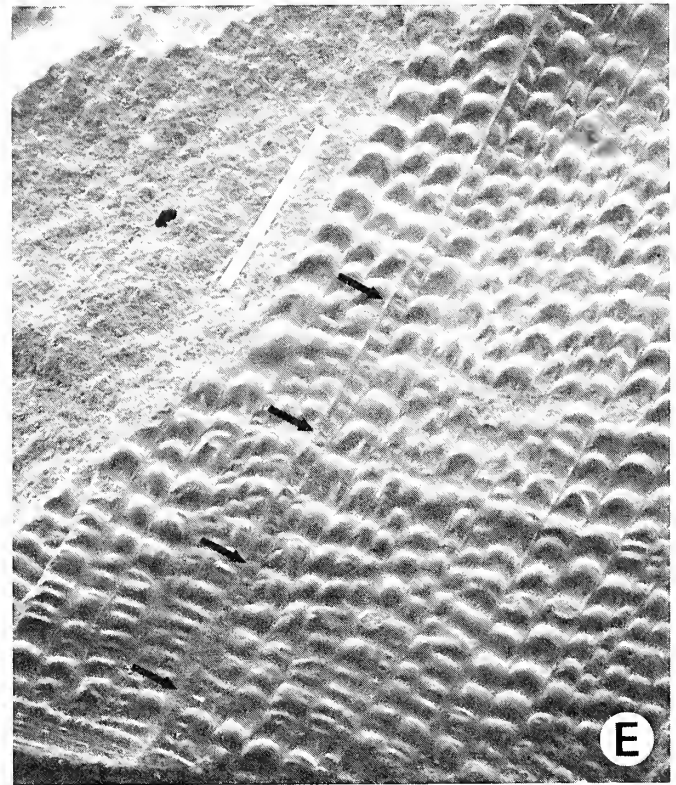
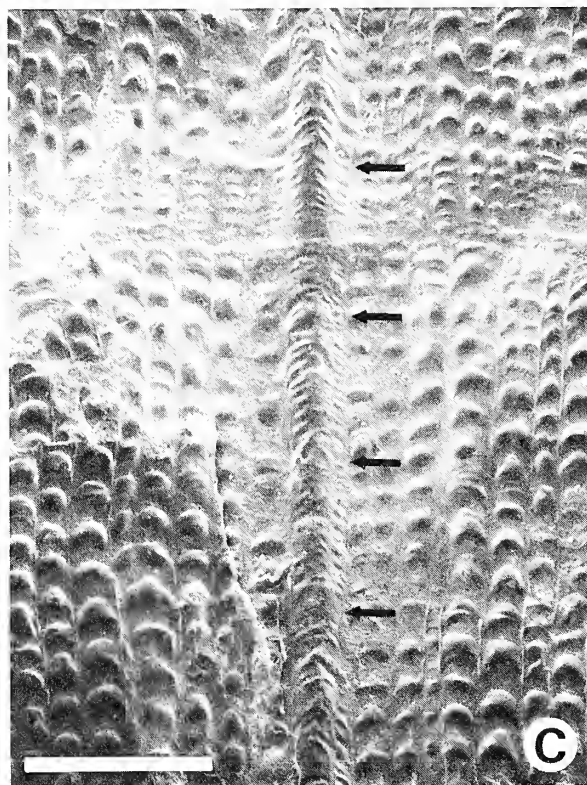
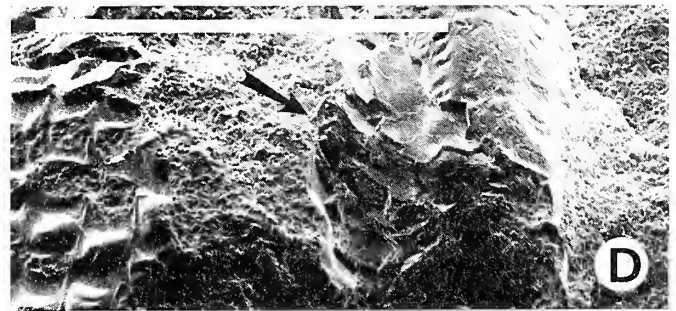
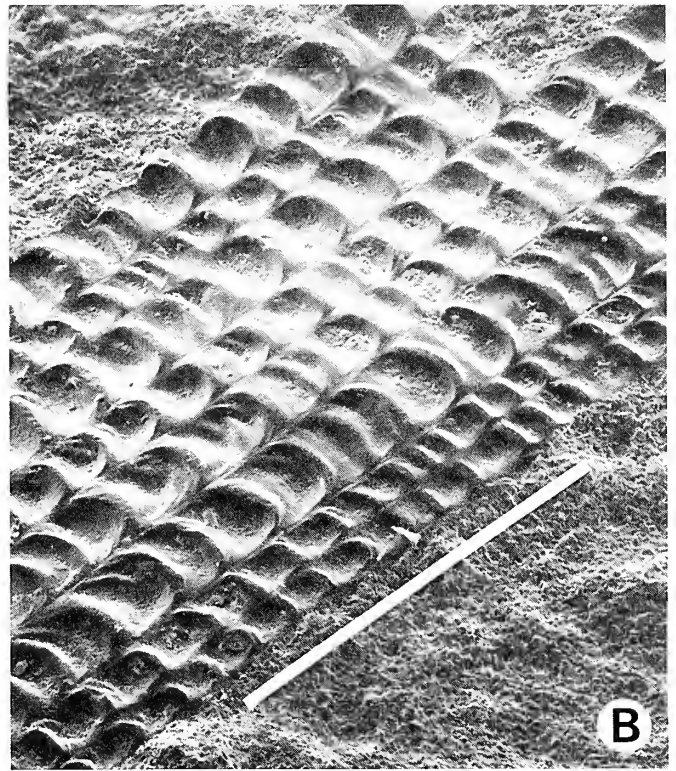
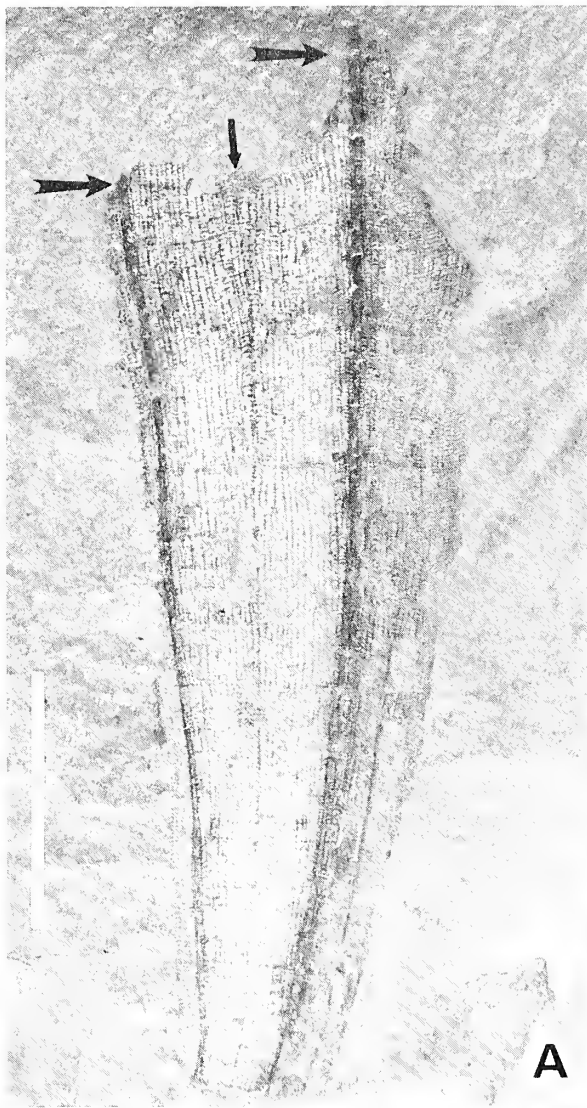
Glyptoconularia gracilis (Hall). SINCLAIR, 1948, p. 268-271, Pl. 10, figs. 1-4; SINCLAIR, 1952, p. 21.

Revised diagnosis.—Conulariids with faces crossed by numerous short, straight or aperturally arching transverse ridges that are arranged in longitudinal files; files bounded laterally by a longitudinal ridge that bears a sharp groove along its crest.

Description.—Test four-sided, straight or gently curved. Corners sulcate, angle of divergence of corners variable or more or less uniform and ranging from approximately 5° to 19°. Midlines marked by a weak groove that is not associated with an internal carina or thickening.

Corners with a strong, continuous internal carina; corner groove crossed by numerous low, transverse ridges that generally arch toward the aperture.

Faces transversely and longitudinally corrugated with numerous short, strong, straight or aperturally arching transverse ridges arranged in distinct longitudinal files. Files bounded by a narrow longitudinal ridge (corrugation) that merges with the ends of the transverse ridges and has a sharp groove along its crest. Number of files increases abapically, with additional files arising by intercalation of new files along the corners (and apparently midlines), and by gradual splitting of a preexisting file into two files that together are slightly wider than their more adapically situated precursor. Individual files generally more or less uniform in width, with the widest files about 2.5 times wider than the narrowest



ones; files range from approximately four to six files per mm.

Transverse ridges normally range from approximately six to ten ridges per mm; transverse ridges in adjacent files offset or aligned transversely, with aligned ridges crossing the faces at right, or nearly right, angles (or close thereto) to the midline. Test may be crossed locally by a band of aligned, rectilinear transverse ridges that are subdued, densely crowded, and show little or no development of a longitudinal ridge between files; some folds extend only partway across a file, usually at a high angle to the midline.

Apex and aperture unknown; schott (apical wall) not observed.

Holotype.—AMNH 796.

Additional specimens.—GSC 94782-94783a-d (at least two specimens), NYSM 5063 (one specimen, a hypotype), SUI 55065-55066 (two specimens), and UMPC 8918 (one specimen). (Note: SUI 55055-55056 and UMPC 8919 do not preserve some of the features (e.g., a groove along the longitudinal ridges) seen in other specimens, but this can be attributed to post-mortem breakage or weathering.)

Horizons and localities.—SUI 55065-55066 and UMPC 8918 are from graptolitic, grey-brown shales near the base of the Maquoketa Formation (Upper Ordovician) in a roadcut near the southwest corner of the village of Graf, Dubuque County, Iowa (see Witzke and Glenister (1987) for additional information on the paleontology and lithostratigraphy of this locality). GSC 94782 is from "shales of Upper Trenton age on the Jacques Cartier River, near Pont Rouge, County Pontneuf [Quebec]" (Sinclair, 1948, p. 269), and GSC 94783 is from "a limestone of Tetreauville age [Tetreauville Formation; see Harland and Pickerill, 1982], 3 miles west of Ste. Elisabeth, County Joliette [Quebec]" (Sinclair, 1948, p. 269). NYSM 5063 is preserved in black, friable Utica Shale from the lower part of the formation, near Dolgeville, New York (Ruedemann, 1896a, 1896b, 1897). AMNH 789 occurs in dark grey lime mudstone and is from the upper part of the Trenton Group (Middle Ordovician) near Middleville, New York (Hall, 1847). This lime mudstone lithology suggests that AMNH 789 was found in the Dolgeville Facies, a unit interpreted by Ross and Bergström (1982) as partly Shermanian in age.

Discussion

Remarks

In his unpublished description of *Glyptoconularia gracilis*, Sinclair (1948) stated that intercalation of new longitudinal files occurs both at corners and at midlines. A possible example of intercalation along a midline is provided by GSC 94783b, which consists mostly of an external mold of parts of two faces (Plate 1, figure E). Examination of this specimen and GSC 94782 (see Sinclair, 1948, Pl. 10, fig. 3), which is also preserved largely as an external mold, suggests that *G. gracilis* midlines have a longitudinal groove that is slightly wider and deeper than longitudinal grooves on either side of the midlines.

Comparisons

As indicated above, *Glyptoconularia gracilis* differs from all other currently recognized conulariids in having faces with narrow longitudinal files of straight or adaperaturally arching transverse ridges. The presence of longitudinal ridges having a sharp groove along their crest also appears to be unique to this species.

Glyptoconularia gracilis is similar to a number of other conulariids (e.g., *Climacoconus* Sinclair, *Conularia* Sowerby, *Conulariella* Bouček, *Conularina* Sinclair, *Eoconularia* Sinclair, and *Paraconularia* Sinclair) in having faces that are transversely corrugated, and it is similar to several transversely corrugated taxa (e.g., *Conularia*, *Malvinoconularia* Babcock et al., and *Reticulaconularia* Babcock and Feldmann) in exhibiting longitudinal corrugation. The longitudinal corrugations (ridges) of *G. gracilis* are most similar to the longitudinal corrugations that cross the interspaces (the region between two adjacent transverse ribs) of *Malvinoconularia* and *Reticulaconularia*. Longitudinal corrugations in the latter two taxa are aligned across the transverse ribs (as opposed to offset, as for example in *Conularia*; see illustrations in Babcock and Feldmann, 1986, and Babcock et al., 1987).

Glyptoconularia gracilis is similar to certain species of *Archaeoconularia* Bouček, *Climacoconus* Sinclair, *Conularina* Sinclair, *Eoconularia* Sinclair, and *Paraconularia* Sinclair in having sulcate corners that are internally carinate. It is further similar to *Archaeoconularia* in having a groove at the midlines, and to *Climacoconus* in having the corner groove crossed by low, closely spaced, adaperaturally arching ridges.

Status of Utica Shale specimens

Inspection of Utica Shale specimens assigned by Ruedemann (1896a, 1896b, 1897) to *Conularia gracilis* Hall yielded only one specimen (NYSM 5063; Ruedemann, 1987, Pl. 2, figures 5-6) that clearly is a conulariid and that belongs to *G. gracilis*. This specimen, approximately 60 mm long, lacks substantial portions of the original test. All of Ruedemann's other specimens either belong to the non-conulariid genus *Sphenothallus* Hall or consist of a minute (less than a few millimeters long) elongate patch of grey-brown material with problematic identity.

Acknowledgments

Permission to borrow or examine museum specimens was provided by T.E. Bolton, N. Eldredge, J. Golden, E. Landing, and W.F. Rice. S.J. Carlson and D.C. Fisher commented on earlier versions of the manuscript. L.E. Babcock, R.M. Feldmann, and E. Landing reviewed submitted versions, and T. Van Iten printed the figures. Funding for this project was provided by the Department of Geological Sciences and the Horace H. Rackham School of Graduate Studies at the University of Michigan, and by NSF Research Grant BNS-8521097 to D.C. Fisher. The scanning electron microscope used in this study was acquired



Plate 1. *Glyptoconularia gracilis* (Hall, 1847). A, AMNH 789, the holotype and most complete specimen (corners marked by large arrows, midline of the most complete face by small arrow; scale bar=1 cm). B-E, scanning electron micrographs of plastic casts of parts of GSC 94873, an apparent single specimen from the Tetreauville Formation (Middle Ordovician, Trentonian), Quebec (all scale bars=1 mm). B, GSC 94873a, fragment preserving the groove along the ridges that bounds the longitudinal files (specimen tilted approximately 30° to the upper left of plate); C, GSC 94873b, part of an external mold of a corner and two faces; note longitudinal file originating along one side of the corner groove (arrows); figure also shows adaperatural splitting of files, and localized crowding and reduction of transverse corrugations and longitudinal ridges between them; D, GSC 94873b, section through a corner carina (arrow; specimen tilted approximately 30° to the top of plate); E, GSC 94873b, external mold of a probable midline (arrows); situated along the right side of the midline is an example of intercalation of a new longitudinal file.

under Grant #BSR-83-14092 from the National Science Foundation. The author personally supplied \$50 toward publication of this report.

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Microstratigraphy and depositional environments of a Middle Devonian foreland basin: Berne and Otsego Members, Mount Marion Formation, eastern New York State

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Abstract

An interval in the shale-dominated lower part of the Mount Marion Formation in eastern New York State has at least twenty-three regionally correlatable event beds and short-term to isochronous faunal and lithologic units within a relatively unfossiliferous, shale-dominated sequence. A local coral-brachiopod biostrome, units with characteristic fossil assemblages, and distinctive sandstone packages allow microstratigraphic subdivision of a 65 m-thick interval of the Formation. Key horizons are traceable south to north (Kingston to Clarksville) for 85 km along depositional strike, and 25 km west into this foreland basin to the Schoharie Valley. Formal names are proposed for four key beds within the interval: the Dave Elliott Bed, Halihan Hill Bed, Katsbaan Bed, and Timmerman Hill Bed. Recognition of a shell-bed-rich shale interval at the base of the Otsego Member in the absence of a locally occurring coral-brachiopod biostrome allows correlation of the previously untraceable base of the Member. Regional lithologic and sedimentologic study indicates that the base of the Otsego Member is somewhat diachronous along the outcrop belt, apparently as a result of erosive beveling associated with a relative lowstand in sea level at the Berne-Otsego Member boundary. A revision of the base of the Otsego Member is proposed; this revision places the base at the base of a coral-brachiopod biostrome or shell-bed-rich shale, and not below a locally underlying, massive sandstone unit.

Introduction

Contemporary stratigraphic analyses of sedimentary basins are increasingly concerned with a finer-scale time-stratigraphic resolution than is possible by means of other stratigraphic methods (e.g., biostratigraphy, magnetostratigraphy, and geochronology). Recognition of widespread cyclic and short-term to isochronous event deposits has led to the development of microstratigraphic analysis and High Resolution Event Stratigraphy (HIRES; *sensu* Kaufmann, 1988). The Cretaceous Western Interior Seaway of North America has been intensively studied by means of these principles. Similar studies have led to a better understanding of some Middle Paleozoic rocks of the northern Appalachian Basin (Brett and Baird, 1986; Brett et al., 1986a, 1990; Miller, 1986, 1990). This report is based on preliminary studies of a Middle Devonian siliciclastic-dominated foreland basin setting in eastern New York State. Previous work on the easternmost marine sediments of the Middle Devonian Hamilton Group has chiefly concentrated on the pale-

ontology and on establishing formation- and member-level stratigraphic subdivisions (Darton, 1894; Prosser, 1894, 1897; Grabau, 1917, 1919; Cooper, 1933, 1941; Chadwick, 1933, 1944; Goldring, 1935, 1943; Lane, 1955). More recent work by Wolff (1967, 1969, 1979) has concentrated on lithologic correlation of units from the Schoharie Valley to the Hudson Valley, and on recognition of the marine to fluvial transition in the Hamilton Group rocks along the Catskill Front (see Figures 1, 2). The purpose of this study has been to determine whether or not relatively thin shell-beds and unique lithostratigraphic packages could be traced section to section through a dominantly unfossiliferous, offshore marine shale interval.

Geological setting

Marine siliciclastic rocks of the Mount Marion Formation (Middle Devonian Hamilton Group) are the basinward part of a prograding clastic wedge that accumulated with erosion of the Acadian Orogen (see Faill, 1985; Woodrow, 1985; Etensohn, 1985a). Lithospheric downwarping associated with tectonic loading (see Etensohn, 1985b; Beaumont et al., 1988), combined with a eustatic sea-level rise (T-R cycle Id of Johnson et al., 1985), ended carbonate deposition of the Onondaga Formation in the northern Appalachian Basin. The lowest units of the Hamilton Group in eastern New York State (Figure 1) consist of a lower black shale (Bakoven Member of Chadwick, 1933) overlain by a thick, calcareous, dark grey to buff-weathering shale and sandstone unit to the south (Stony Hollow Member of Cooper, *in* Goldring, 1943), and a thin carbonate unit to the north (Cherry Valley Limestone of Clarke, 1903). Overlying black to dark grey shales record an abrupt deepening event (T-R cycle Ie of Johnson et al., 1985) at the base of the Mount Marion Formation ("Mount Marion Beds" of Grabau, 1917, 1919, p. 470). The lower part (ca. 85 m) of the Formation (Berne Member of Cooper, 1933; revised by G.A. Cooper, *in* Goldring, 1943) consists of dark clay shales with a fauna dominated by low-diversity *Leiorhynchus* and nuculid bivalve-cephalopod associations. The top of the Berne Member is defined locally by a coral-brachiopod biostrome at the base of the Otsego Member (Cooper, 1933). Dark grey silty shales with abundant sideritic(?) nodules, greater sand content, and medium- to high-diversity brachiopod-dominated faunas characterize the lower part of the Otsego Member. A general coarsening-up succession from silty shales to nearshore, reworked, quartz-rich sandstones marks the upper part of the Mount Marion Formation.

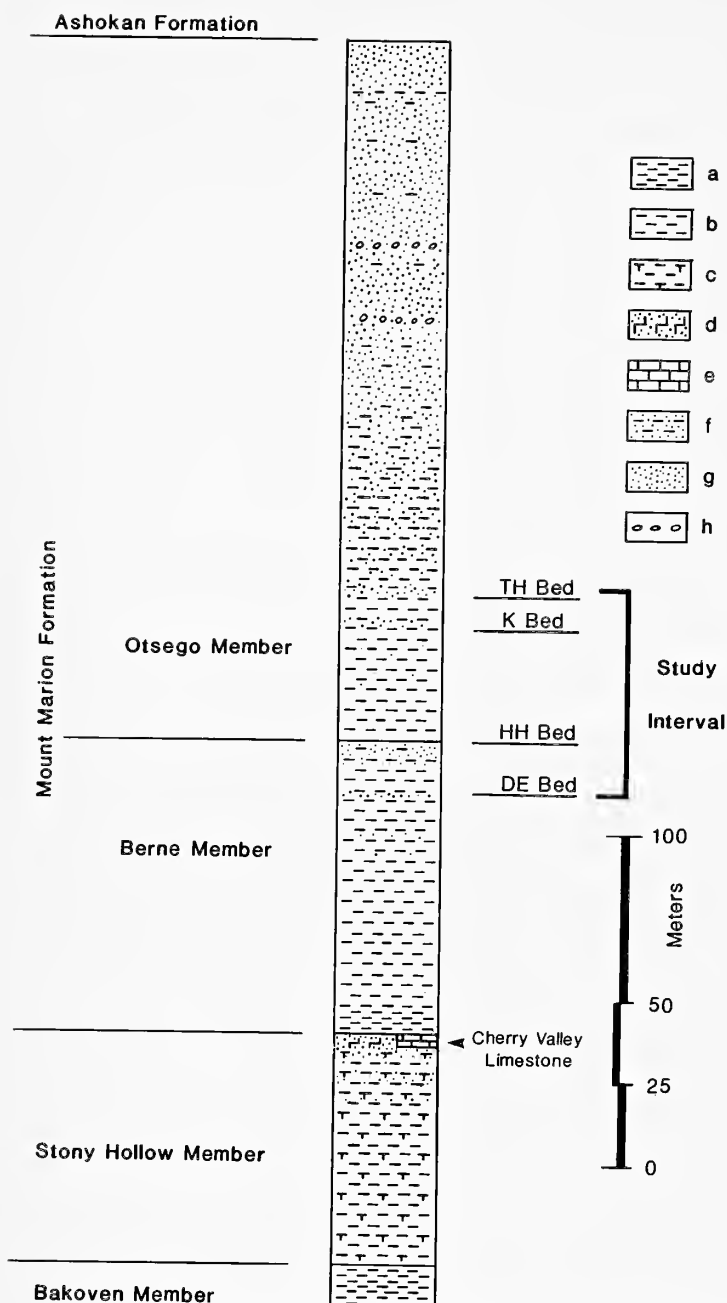


Figure 1. Generalized section of the Mount Marion Formation and associated strata. Explanation: a, black shales; b, dark grey shales; c, calcareous shales and thin-bedded, argillaceous limestones; d, calcareous sandstone; e, limestone; f, sandy shale to shaly sandstone; g, sandstone; h, quartz and chert pebble conglomerate. Abbreviations: DE Bed=Dave Elliot Bed; HH Bed=Halihan Hill Bed; K Bed=Katsbaan Bed; TH Bed=Timmerman Hill Bed.

Methods

Exposures through a 65 m section in the upper part of the Berne Member and lower part of the Otsego Member of the Mount Marion Formation were measured and studied along 110 km of the outcrop belt in eastern New York State (Figure 2). Four major key beds were recognized. In addition, up to nineteen other traceable faunal and lithostratigraphic marker units were found. These units were initially correlated

through ten sections along 26 km of the outcrop belt in the Rhinebeck, Kaaterskill, and Catskill 15-minute Quadrangles. Subsequent work extended these correlations 59 km farther north across the Cossackie and Albany 15-minute Quadrangles and 25 km west through the Berne and Schoharie Quadrangles. Thin shell-beds (ca. 0.01 to 1 m thick, some of which may represent a series of amalgamated beds) separated by relatively thick shale intervals (ca. 1.0 to 8.0 m), and packages of thin sandstone beds, allow microstratigraphic subdivision of the Berne and Otsego Members through the study interval.

Revision of the base of the Otsego Member

Cooper (1933, p. 549) defined the base of the Otsego Member at the bottom of a coral- and brachiopod-rich interval that he named the "*Meristella*-coral Zone." The base of the Otsego Member was not traced by Cooper along the outcrop belt in the Hudson Valley because the coral-rich facies was absent. During the course of this study, an interval of shale with numerous shell-beds was found to lie at the base of the Otsego Member where the coral-rich unit is absent, and its presence allows delineation of a traceable base for the Otsego Member.

Cooper (see Goldring, 1935, pp. 189, 190) defined the *Meristella*-coral Zone near East Berne (Loc. 15 of this report; see Figure 2) as a 3.0 m-thick, richly fossiliferous interval. A meter-thick coral bed lies above a 1.2 m-thick, fossiliferous, massive sandstone at the base of the Zone. The sandstone unit, which may range up to five or more meters in thickness, is not present along the entire outcrop belt; north of Kingston (Locs. 2, 3, 4, and 6), the coral bed lies on dark grey silty shales. The revision of the boundary between the Berne and Otsego Members proposed below defines a contact between the two members that is less diachronous, although still somewhat so. A mappable base for the Otsego Member in this region can be defined at four levels, depending on the section: (1) at the base of the coral-rich facies of Cooper's (1933) *Meristella*-coral Zone; (2) at the lowest occurrence of rugose corals in a massive sandstone (up to 5.0 m thick) that represents amalgamation of the massive sandstone with the overlying coral unit; (3) at the top of this massive sandstone where rugose corals are not present; or (4) at the lowest *Mediospirifer*-rich shale bed that overlies a package of intercalated thin sandstones and shales (ca. 8.0 m thick) where the coral bed and massive sandstone are absent.

Units used for correlation

Formally named marker beds

Dave Elliott Bed (new).—The name "Dave Elliott Bed" is proposed for a fossiliferous unit that generally lies 13-15 m below the top of the Berne Member. The type section is in a small quarry along Dave Elliott Road north of Saugerties (Loc. 9), where an 18 cm-thick sandstone bed underlies a westward-dipping surface near the center of the quarry (Figure 3B). The Dave Elliott Bed is typically a buff-weathering, fine- to medium-grained, highly burrowed or bioturbated sandstone up to 1.5 m thick. A rusty-weathering silty shale interval up to 1.0 m thick characterizes the unit at the southern end of the study area (Loc. 2, Figure 2). Brachiopods, dominated by small *Devonochonetes* with or without spiriferids, typify the fauna. This fauna changes northward into a higher-diversity association that includes some rugose corals; this increase in diversity is accompanied by thickening of the sandstone. Original sedimentary structures are generally obliterated by intense burrowing.

The bed is sometimes underlain by a horizon of bulbous to elongate nodules (see Figure 3A).

Halihan Hill Bed (new).—Cooper (1933; G.A. Cooper, in Goldring, 1943, p. 249) noted the presence of a richly fossiliferous coral-brachiopod biostrome in the Schoharie, East Berne, and Kingston areas, which he used to define the base of the Otsego Member. The paleontology and stratigraphy of the coral-rich unit were treated in detail by Lane (1955). The name “Halihan Hill Bed” is proposed for the coral-rich bed of Cooper’s (1933) *Meristella*-coral Zone. The type section is along New York Rte. 209 (Loc. 2), 0.6 km south of Halihan Hill, where 50 cm of a highly fossiliferous coral-rich bed is exposed in the bank above the highway (Figure 3F). A crinoidal, debris-rich, silty limestone to calcareous shale rests with a sharp contact on unfossiliferous shale at this locality. This same unit at East Berne (Loc. 15) rests on a massive sandstone unit. Between Localities 8 and 15, the coral bed is not present. A high-diversity fauna dominated by rugosans characterizes the coral bed. Lane (1955) listed fifteen species of rugose and tabulate corals from the coral-rich Halihan Hill Bed. He also noted twenty-seven other forms, dominantly brachiopods (including *Mediospirifer*, *Pseudoatrypa*, *Elita*, *Athyris*, and *Nucleospira*). Additional elements of the fauna include lacy and branching bryozoans, the bivalves *Paleoneilo* and *Nyassa*, two gastropods, the trilobite *Phacops rana*, and crinoidal debris.

Katsbaan Bed (new).—A meter-thick, dark grey- to brown-weathering, bioturbated siltstone unit approximately 33 m above the Halihan Hill Bed is a key marker bed that is traceable along much of the outcrop belt. The name “Katsbaan Bed” is proposed for this unit for its type locality along New York Rte. 32, 1.5 km northwest of Katsbaan on the Catskill 15-minute Quadrangle (Loc. 7; Figure 3C). Upper and lower boundaries of the unit are generally gradational with the surrounding silty shales. This unit features the lowest diverse bivalve fauna in the Mount Marion Formation; taxa include pectenoid and pterinoid bivalves, with *Modiomorpha*, *Goniophora*, and *Paracyclas*, among others. Numerous paleozygopleuriid gastropods and bellerophonts occur along with nautiloid and goniatitic cephalopods, branching bryozoans, crinoidal debris, and traces. The diverse brachiopod fauna includes *Spinocyrtia*, *Paraspirifer*, *Protoleptostrophia*, and *Productella*.

Timmerman Hill Bed (new).—The top of the interval studied is a massive, brown-weathering, highly fossiliferous, *Zoophycos*-churned sandstone that is generally on the order of 2.5 m thick. This unit is designated the “Timmerman Hill Bed” (Figure 3E). The sandstone forms the caprock of High Falls (Loc. 10; Figure 3H) on Kaaterskill Creek at the southern end of Timmerman Hill (Catskill 15-minute Quadrangle). The unit contains a high-diversity fauna similar to that of the Katsbaan Bed. However, the forms tend to be more robust, and many shells exhibit extensive *Vermiforichnus* borings. Local to widespread rugose corals, rostroconchs, and the crinoid bulb-like holdfast *Ancyrocrinus* can also be present. Prominent wave ripples and dune structures occur on the upper surface of the Timmerman Hill Bed at High Falls.

Thin sandstone packages

Distinctive bundles of 2-50 cm-thick sandstone beds are found at five different levels within the upper part of the Berne Member and lower part of the Otsego Member of the Mount Marion Formation. Internal structures of the thin sandstone beds include finely laminated planar bedding to hummocky cross-stratification. Wave-produced bidirectional cross-sets and ripple structures may be present. The beds generally exhibit sharp basal contacts and may also feature weakly developed current lineations (groove casts) on the soles. Burrowing within these beds is generally sparse to nonexistent. Apparent vertical

escape burrows are locally present and suggest rapid deposition of these thin sandstone beds. Subhorizontal traces may occur at or near the tops of the thin sandstone beds (see Figure 4E).

An approximately 8.0 m-thick package of thin sandstones and shales is locally present at the top of the Berne Member. This interval is overlain to the north by a thick-bedded to massive fossiliferous sandstone that is, in turn, overlain by additional thin sandstone beds. The package shown in Figure 4D, which is found near the top of the interval studied, displays the characteristic thin siltstone to sandstone beds and interbedded shales.

Distinctive faunal association intervals

Mediospirifer beds.—Beds dominated by *Mediospirifer*, with or without *Athyris*, generally characterize the lower part (ca. 24 m) of the Otsego Member (Figure 4A). *Mediospirifer* beds range in thickness from several centimeters to 0.5 m, and individual beds may include multiple shell layers. These beds are often correlatable for considerable distances between localities along the outcrop belt. A key *Mediospirifer* bed is present on the top of the coral-brachiopod biostrome, and another occurs 6.0 to 9.0 m above it. These beds often include articulated shells in association with disarticulated valves that may exhibit abrasion. Small phosphatic pebbles appear in some beds, along with occasional fish debris.

Eumetabolotoechia beds.—Shale-rich beds with low-diversity faunas dominated by the brachiopod *Eumetabolotoechia multicostum* may be found overlying the *Mediospirifer* bed that rests on the coral biostrome of the Halihan Hill Bed. The associated fauna may include cephalopods (*Orthoceras*?) and small infaunal bivalves (*Nucula*, *Nuculites*, and *Paleoneilo*), in addition to plant debris.

Cephalopod-rich intervals.—One type of unique fossil occurrence is represented by cephalopod-rich intervals. A horizon of this type, which features small goniatitic cephalopods (*Parodiceras*?, ca. 3.0-4.0 cm in diameter), lies approximately 3.0 m above the Halihan Hill Bed. Another cephalopod-rich unit with orthoconic nautiloids (*Orthoceras*?) lies in an interval approximately 22 m above the Halihan Hill Bed. The bryozoan *Reptaria* is commonly found colonizing the cephalopod conchs in this unit. Two key *Mediospirifer* beds are always found to lie approximately 4.0 m below and 0.5 m above this interval.

Cranaena beds.—Very thin, widespread shell beds with characteristic faunal elements also form key marker horizons. Two such horizons feature abundant specimens of the small terebratulid brachiopod *Cranaena*. One of these horizons generally occurs 4.0-8.0 m above the base of the Otsego Member, and another always immediately underlies the Katsbaan Bed throughout the study area (see Figures 3C, 3D). These beds vary in diversity from an almost monospecific *Cranaena*-rich shell layer to beds with as many as ten genera. These assemblages may include the brachiopods *Mediospirifer*, *Mucrospirifer*, and *Ambocoelia*, along with small *Devonochonetes* and *Rhipidomella*. Orthoconic cephalopods, small bivalves, and the gastropod *Bembexia* may be present as well. *Cranaena* disappears from the lower bed at the more marginal southern and western localities where *Ambocoelia* is the dominant brachiopod present.

Mucrospirifer beds.—Thin beds (ca. 2.0-5.0 cm) dominated by *Mucrospirifer* may occur in an interval 30 to 40 m above the Halihan Hill Bed. The fauna of these beds, in addition to *Mucrospirifer*, includes *Mediospirifer*, *Protoleptostrophia*, *Devonochonetes coronatus*, and other small *Devonochonetes*. *Tentaculites*, the gastropod *Bembexia*, and conulariids may also occur locally. Crinoidal debris and shell hash is commonly present in the beds, and small phosphatic pebbles may also occur.

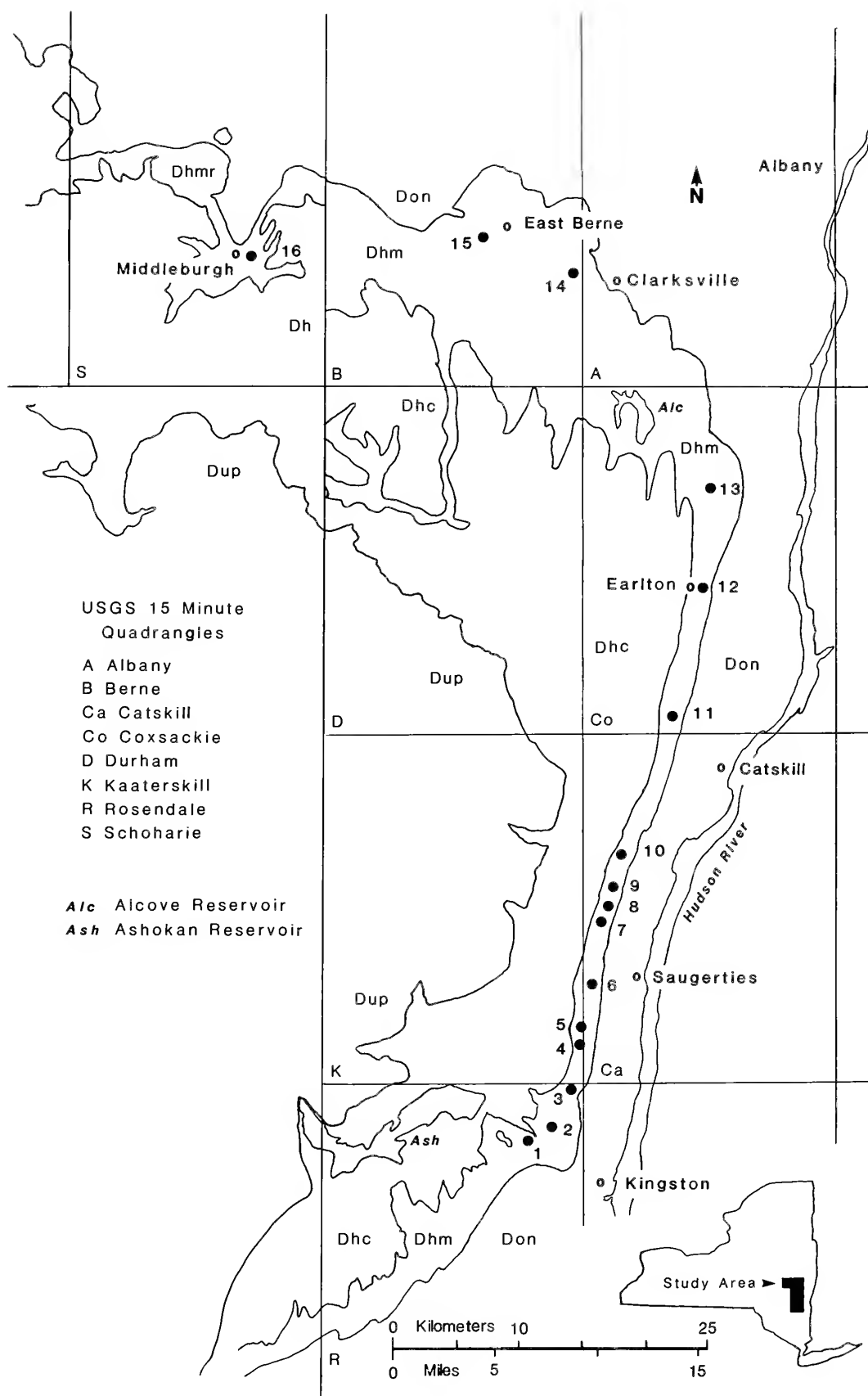
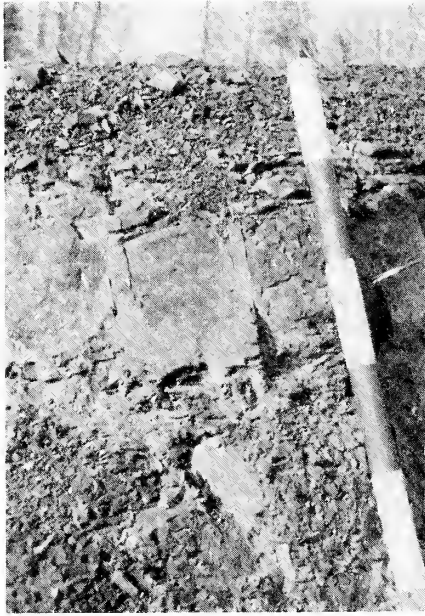


Figure 2. Generalized geologic and locality map. Geologic map modified from Fisher et al. (1970). Explanation: (Don) Onondaga Limestone and lower units; (Dhm) Mount Marion Formation and associated strata, including Panther Mountain Formation to north (Hamilton Group); (Dhmr) Marcellus Formation (Hamilton Group); (Dh) Panther Mountain and Moscow Formations (Hamilton Group); (Dhc) Continental facies of the Hamilton Group; (Dup) Upper Devonian rocks. Localities: (1) Roadcut on Jockey Hill Road, and quarry along New York Rte. 28, 2 and 3 km northwest of New York Rte. 209; (2) Roadcuts along New York Rte. 209, between New York Rte. 28 and Sawkill Road; (3) Quarries on east side of Halihan Hill, along Ulster Co. Rte. 31; (4) Small quarry and cliff along Schoolhouse Road, 1.3 km north-east of Ruby; (5) Exposure along Plattekill Creek at bridge, 0.3 km west of Mount Marion village; (6) Large quarry on Mount Marion, 0.5 km south of Veteran; (7) Roadcut along New York Rte. 32, 1.5 km northwest of Katsbaan; (8) Quarry along Shear Road, 1.2 km northeast of Quarryville; (9) Quarry and ravine along Dave Elliott Road, 1.0 km north of Locality 8; (10) Exposures at High Falls, and roadcut and quarry 0.5 km northeast; (11) Roadcut along Sandy Plains Road, 1.3 km north-west of Leeds; (12) Quarries 1.0 km east of Earleton; (13) Stream cut south of Stanton Hill Cemetery, 4.6 km southeast of Coeymans Hollow village; (14) Top of ravine along Hannaeris Creek, off Duck Hill Road, 1.7 km SSE of Helderberg Lake; (15) Roadcut along Cole Hill Road, 2.0 km southwest of East Berne; (16) High bank along Stony Creek, "The Gorge," Middleburgh.



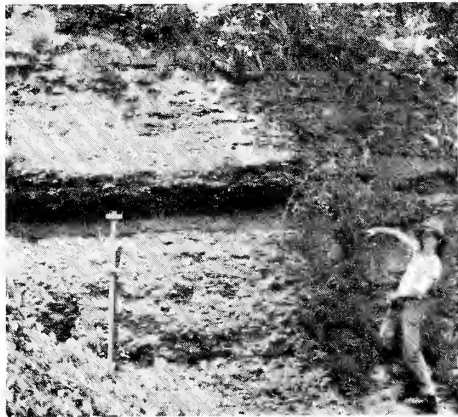
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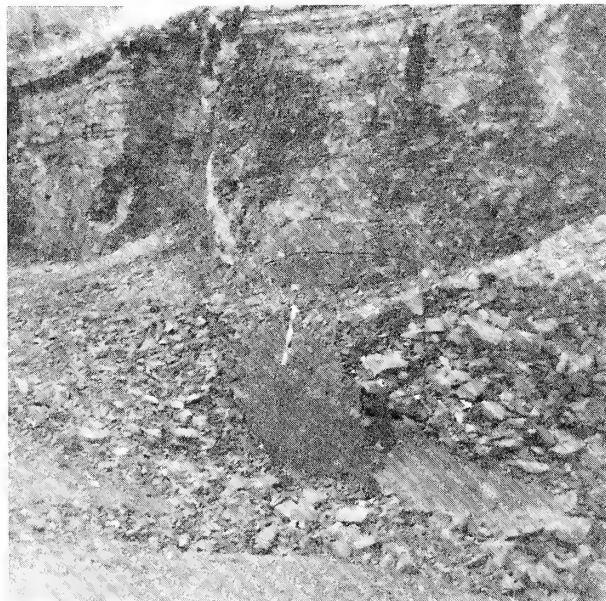
D



E



F



G



H

Figure 3. The four formally named beds in the Berne and Otsego Members of the Mount Marion Formation. *A*, Bulbous nodules that locally underlie the Dave Elliott Bed in the study area; nodules may also be more vertically elongated. Coin measures 19 mm across. *B*, Highly burrowed, fine- to medium-grained sandstone of the Dave Elliott Bed at its type locality (Loc. 9). Scale equals 0.5 m. *C*, Katsbaan Bed at its type locality (Loc. 7); the arrow points to the thin, persistent *Cranaena* bed. Jacob's staff is 1.5 m long. *D*, Katsbaan Bed at Locality 15; the author points to the thin *Cranaena* bed. Jacob's staff measures 1.5 m. *E*, The 2.5 m-thick massive *Zoophycos*-churned sandstone of the Timmerman Hill Bed at Locality 7. Note 10 cm subdivisions of measuring stick. *F*, Coral-rich facies of the Halihan Hill Bed at Locality 2 (type locality); the coral-rich unit (0.5 m thick) extends from base of hammer to pencil. Pencil lies at base of 10.0 cm-thick *Mediospirifer*-dominated bed. *G*, Shell-bed-rich shale facies of the Halihan Hill Bed at Locality 11. Black and white staff measures 0.5 m. *H*, Timmerman Hill and Katsbaan Beds at High Falls (Loc. 10); the 2.5 m-thick Timmerman Hill Bed forms the caprock of the falls.

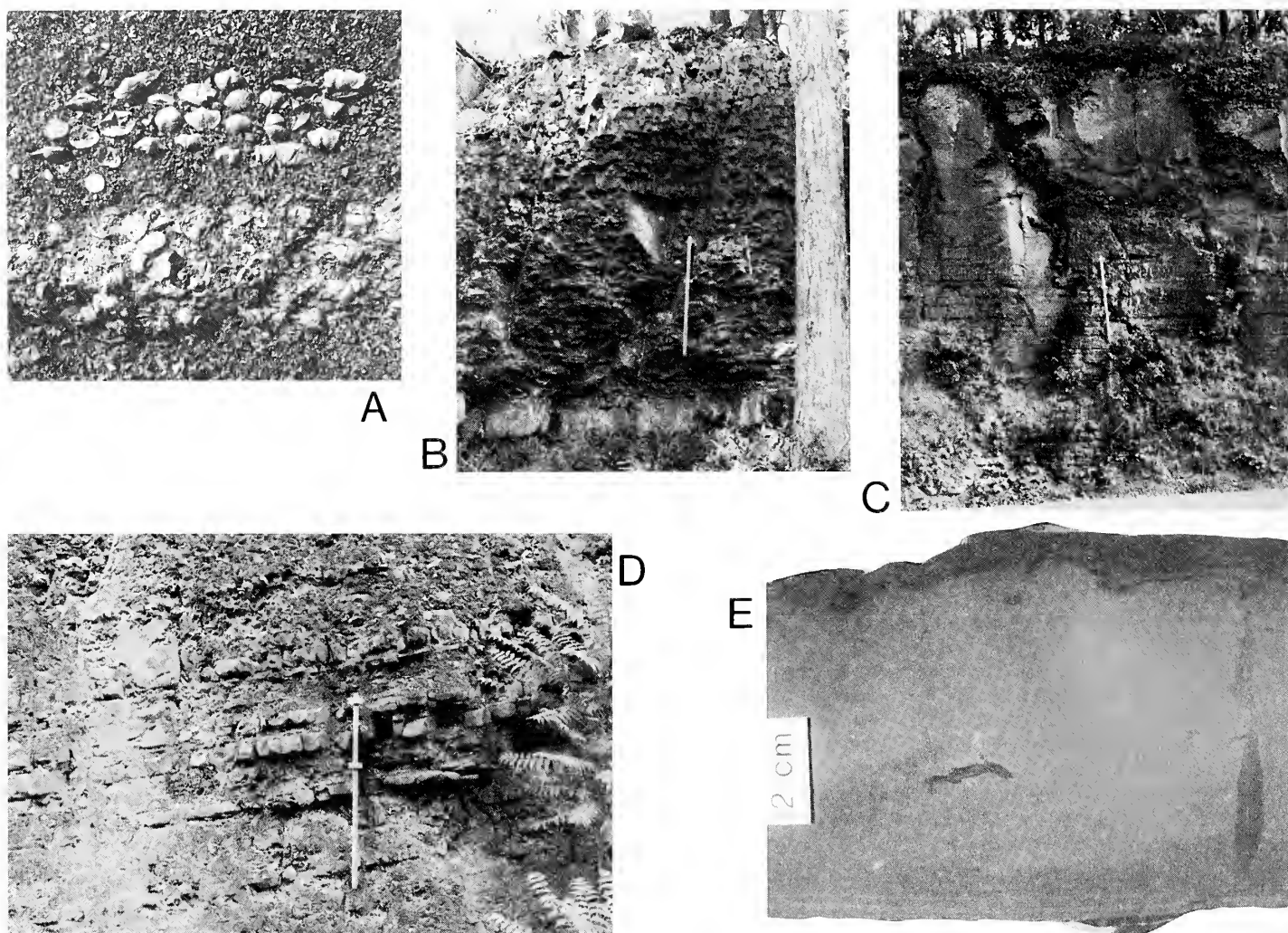


Figure 4. Sandstone packages and shell bed from the Berne and Otsego Members of the Mount Marion Formation. *A*, *Mediospirifer*-dominated bed 31 m above the Halihan Hill Bed at Locality 3 shows shell bed and typical fauna. Coin is 18 mm in diameter. *B*, Thick-bedded to massive sandstone below Halihan Hill Bed at Locality 14; note 0.5 m-thick tempestite bed at base. Jacob's staff measures 1.5 m. *C*, Thick-bedded to massive sandstone below Halihan Hill Bed and underlying thin sandstones, at intersection of New York Rtes. 85 and 443 between Localities 14 and 15. Jacob's staff measures 1.5 m. *D*, Thin sandstone package at Locality 7 shows typical alternations of thin siltstone to sandstone beds with interbedded shales. Jacob's staff is 1.5 m long. *E*, Slab of a thin sandstone bed with finely laminated planar bedding, an apparent vertical escape burrow, and sub-horizontal traces near the top of the bed.

Interbedded shales

Dark grey, blocky-weathering, argillaceous to silty shales compose intervals that measure approximately 1.0-8.0 m thick in the study area. The shales between the shell beds generally lack skeletal materials and typically appear featureless, with few, if any, visible sedimentary structures. Slabs of several thin intervals of the shales indicate a moderate to high degree of burrowing that includes *Chondrites* burrows. The upper part of the study interval (ca. 40 m) also features numerous horizons of small sideritic(?) nodules. The nodules are generally unfossiliferous, though a few horizons may include a shelly fauna or traces.

Discussion

Correlations in southern part of field area

Figure 5 shows the faunal and lithostratigraphic correlations for ten

sites along a 16 km interval of the outcrop belt on the Rhinebeck, Kaaterskill, and Catskill 15-minute Quadrangles (e.g., from Kingston to south of Catskill, trending roughly north-northeast). Twenty correlatable horizons are traceable between the sections; Figure 5 indicates a predictable sequence of faunas and lithofacies from site to site.

Lateral changes in faunas and lithologies may be noted for the key horizons across the local outcrop area. A key change is the pinchout of the coral-brachiopod biostrome of the Halihan Hill Bed northward across the Catskill 15-minute Quadrangle. At its most northerly occurrence in this area (Loc. 8), the coral unit appears as a thin *Mediospirifer*-dominated bed within a silty shale. A few scattered small rugosans, some apparently corroded prior to burial, are accompanied by crinoidal debris-rich clasts of the same lithology, as in exposures of the coral bed to the south. *Mediospirifer* beds without corals characterize this interval at Localities 9 and 10.

On the other hand, general northward thickening and coarsening

trends characterize the Dave Elliott, Katsbaan, and Timmerman Hill Beds in the southern part of the field area. The Dave Elliott Bed changes northward from a meter-thick unit of silty shale at the southern edge of the outcrop belt (Loc. 2) to the more characteristic highly burrowed, fossiliferous sandstone facies seen at Locality 9 (see Figure 3B). Faunal diversity also tends to rise northward in the different units, and this is accompanied by some changes in the faunal associations. These changes include the replacement of the *Eumetabolotoechia* bed above the Halihan Hill Bed by a *Mediospirifer*-dominated fauna.

Vertical lithologic changes to the top of the Berne Member reflect an increase in grain size that culminates in an 8.0 m-thick package of thin siltstone to sandstone beds. Associated faunal changes through the upper part of the Berne Member are characterized by an increase in diversity and a trend toward faunas of relatively more aerobic/shallow-water aspect. These changes culminate in the Halihan Hill Bed at the base of the Otsego Member. The Halihan Hill Bed is overlain by a relatively thin interval (ca. 3.0–4.0 m) that features both an upward fining in lithology and a gradational change in faunas into those of lower diversi-

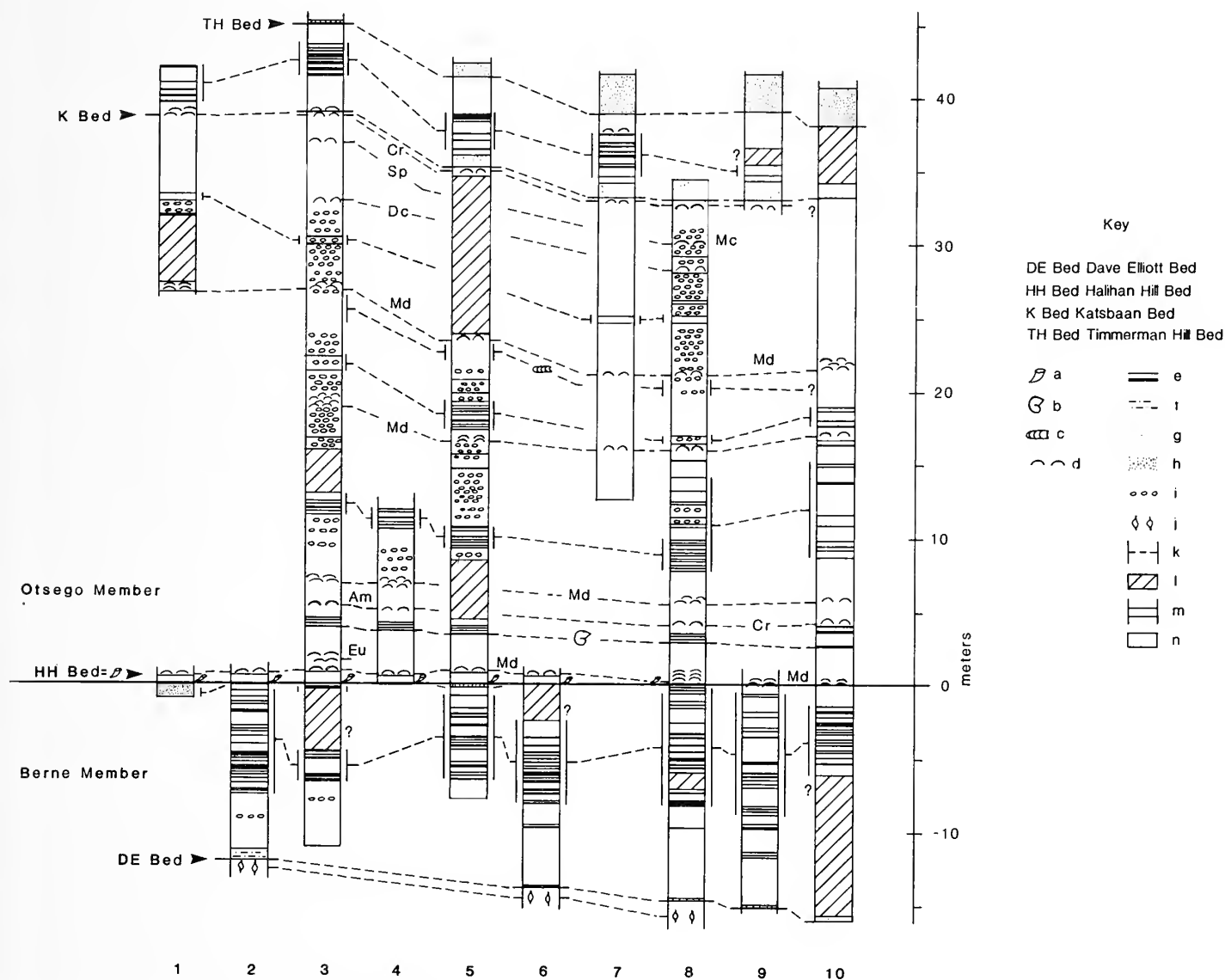


Figure 5. Correlations in southern part of field area. Nodular intervals not shown for Localities 7, 9, and 10. Explanation: a, coral-brachiopod biostrome; b, goniatite bed; c, orthoconic cephalopod interval; d, shell bed; e, *Ambocoelia* bed; f, *Cranaena* bed; g, *Devonochonetes* bed; h, *Eumetabolotoechia multicosum* bed; i, *Mucrospirifer* bed; j, *Mediospirifer* bed; k, *Spinocyrtia* bed; l, thin siltstone to sandstone beds; m, silty shale (facies of Dave Elliott Bed); n, siltstone; o, sandstone; p, sideritic nodules; q, bulbous to elongate nodules; r, correlatable packages; s, covered or inaccessible interval; t, outcrop continues above/below; u, outcrop covered above/below.

ty and more dysaerobic/deeper-water aspect (e.g., a *Mediospirifer* bed overlain by a *Eumetabolotoechia multicosum* bed.)

The overlying part of the study interval in the Otsego Member again displays a general upward coarsening, with the appearance of faunas of increasing diversity and of shallower-water aspect. *Mediospirifer* beds of low- to medium diversity dominate the lower 24 m of the section that overlies the Halihan Hill Bed. This is overlain by a thin interval with *Mucrospirifer*-dominated beds, which is, in turn, succeeded by the relatively highly diverse Katsbaan and Timmerman Hill Beds with *Spinocyrtia*, *Paraspirifer*, and a diverse bivalve fauna. These faunal changes are associated with a general coarsening-up trend that culminates in the thick, massive sandstone of the Timmerman Hill Bed.

Regional correlations

Figure 6 shows correlations for the upper part of the Berne Member and lower part of the Otsego Member along 110 km of the outcrop belt. These correlations extend northward roughly along depositional strike from Kingston to Clarksville, and basinward to the west as far as the Schoharie Valley. As shown, key marker horizons are often traceable for great distances along the outcrop belt. Some of the thinner units either persist across the region or may disappear locally only to reappear farther along the outcrop, whereas others have not been found and may or may not be present.

The Dave Elliott Bed continues to thicken northward of Locality 10 to a thickness of approximately 1.5 m at Localities 12 and 13. A rise in faunal diversity parallels this thickening trend; several medium-sized rugose corals and numerous other forms were noted at Locality 12. At Hannacrois Ravine (Loc. 14), the Dave Elliott Bed is thinner (ca. 70 cm) and is underlain by a horizon of bulbous nodules as seen in outcrops to the south. Faunal diversity is lower than at Localities 12 and 13, but the unit is still highly bioturbated and features numerous small *Devonochonetes*, *Eumetabolotoechia multicosum*, and conulariids, along with small bivalves and cephalopods.

Thin sandstones that underlie the Halihan Hill Bed to the south are overlain northward by a thick-bedded to massive sandstone unit that is best seen in an anomalously thick section at Locality 14 at the top of Hannacrois Ravine near Clarksville (Figure 4B). Five meters of brown-weathering, bioturbated sandstone mark the upper part of the Berne Member at this locality, with a layer 20 cm below the cap of the sandstone that features rugose corals (=base of the Otsego Member). Small *Devonochonetes*, along with *Mediospirifer* and occasional *Protoleptostrophia* and linguloid brachiopods, are common in the massive sandstone unit. Bivalves, including *Modiella*, *Grammysia* and *Cornellites*, occur locally, and orthoconic cephalopods and conulariids may be present. *Tentaculites* is present in the massive sandstone at Localities 12 and 13 and occurs with the brachiopod *Cupulorostrum* at Locality 12. (The latter two genera are not generally found below the Timmerman Hill Bed.) The thick-bedded to massive sandstone unit is generally underlain by a package of thin siltstone to sandstone beds (Figure 4C), as below the Halihan Hill Bed to the south. A partly covered section at Locality 13 features the massive, bioturbated sandstone above a thick, massive unit of thin-bedded sandstone.

The coral-brachiopod biostrome of the Halihan Hill Bed pinches out north of Locality 8, and the lower part of the Otsego Member is represented by an interval of *Mediospirifer* shell-bed-rich shales that ranges up to approximately 4.0–5.0 m in thickness. These shale-rich strata characterize the base of the Otsego Member for approximately 64 km between Localities 8 and 15. However, the coral-brachiopod biostrome reappears at East Berne (Loc. 15) as a meter-thick, richly fossiliferous

unit overlain by a thin (ca. 10 cm-thick) *Mediospirifer*–*Athyris* bed, which is, itself, followed by *Eumetabolotoechia*-rich shale. This local sequence resembles that at Locality 3.

At the most easterly and basinward site at Middleburgh (Loc. 16), the Halihan Hill Bed is found several meters above the base of a 34 m-thick section along Stony Creek. It is represented here by a 23 cm-thick bed with rugose corals that lies near the middle of a 3.0 m-thick richly fossiliferous, dark grey silty shale interval. More than fifty genera were counted in the field with C.E. Brett for the entire interval inclusive of the coral bed. These include rugosan and tabulate corals (five genera), pelecypods (16), brachiopods (15), gastropods (3), a bellerophonid, cephalopods (3), bryozoans (2), a phacopid trilobite, a crinoid calyx and ossicles, and several traces (see also Brett et al., 1990, Tab. 2). Black shale dominates the overlying section nearly to the top, and none of the other correlatable units have yet been recognized at Locality 16.

Brett and Landing (in Anderson et al., 1988, p. 133) reported an occurrence of the “*Meristella*-coral Zone” at a locality near Rensselaerville, in the Berne 15-minute Quadrangle. This coral bed, which has been found at several other localities in the Schoharie 15-minute Quadrangle, is not the same unit but lies much higher (ca. 300 m), either in the upper part of the Mount Marion Formation or in the lower part of the overlying Panther Mountain Formation.

Figure 3D shows the Katsbaan Bed at Cole Hill near East Berne (Loc. 15). The figure shows the author pointing to the persistent *Cranaena* bed that underlies the nearly 1.0 m-thick Katsbaan Bed. The fauna here again features *Spinocyrtia* and *Protoleptostrophia*, with several bivalves and *Zoophycos* traces. At Earlton (Loc. 12), the Katsbaan Bed and the associated *Cranaena* bed overlie a hard, massive sandstone that forms a long platform near the top of the main quarry.

The Timmerman Hill Bed is covered at several key sites in the northern part of the outcrop belt but is present at the top of the quarry at Earlton (Loc. 12). This massive sandstone has thinned to approximately 1.5 m at this locality, but it contains a more diverse fauna than at localities to the south.

Units at the Berne–Otsego Member contact

The boundary interval of the Berne and Otsego Members is characterized along the outcrop belt by four distinct units: (1) a package of intercalated thin sandstones and shales (upper Berne Member); (2) a massive, bioturbated sandstone unit that ranges up to 5 m thick (uppermost Berne Member); (3) the coral-brachiopod biostrome of the Halihan Hill Bed (lowest Otsego Member); and (4) a shale interval with numerous *Mediospirifer*-dominated shell beds (lower Otsego Member). At localities where the massive sandstone (unit 2) is missing along the outcrop belt (between Loc. 1 and approximately 7.0 km south of Loc. 12), the top of the Berne Member is characterized by a package of thin sandstones and shales (unit 1). At localities where the Halihan Hill Bed (unit 3) is missing (between Locs. 8 and 15), the lowest part of the Otsego Member features the shell-bed-rich shale interval (unit 4).

Detailed study of this Berne–Otsego boundary interval along the outcrop belt appears to indicate that a composite section of the boundary interval would feature a vertical sequence from units 1 through 4; this is similar to the section at Locality 15 (near East Berne). In the vicinity of East Berne, a package of thin sandstones and shales is successively overlain by the massive sandstone unit and then by the meter-thick Halihan Hill Bed. The Halihan Hill Bed at East Berne underlies dark shales with brachiopod-dominated beds. Between Localities 15 and 8, the coral facies is not present (see Figure 6), and the overlying shell-bed-rich shales of unit 4 overlie the massive sandstone. The mas-

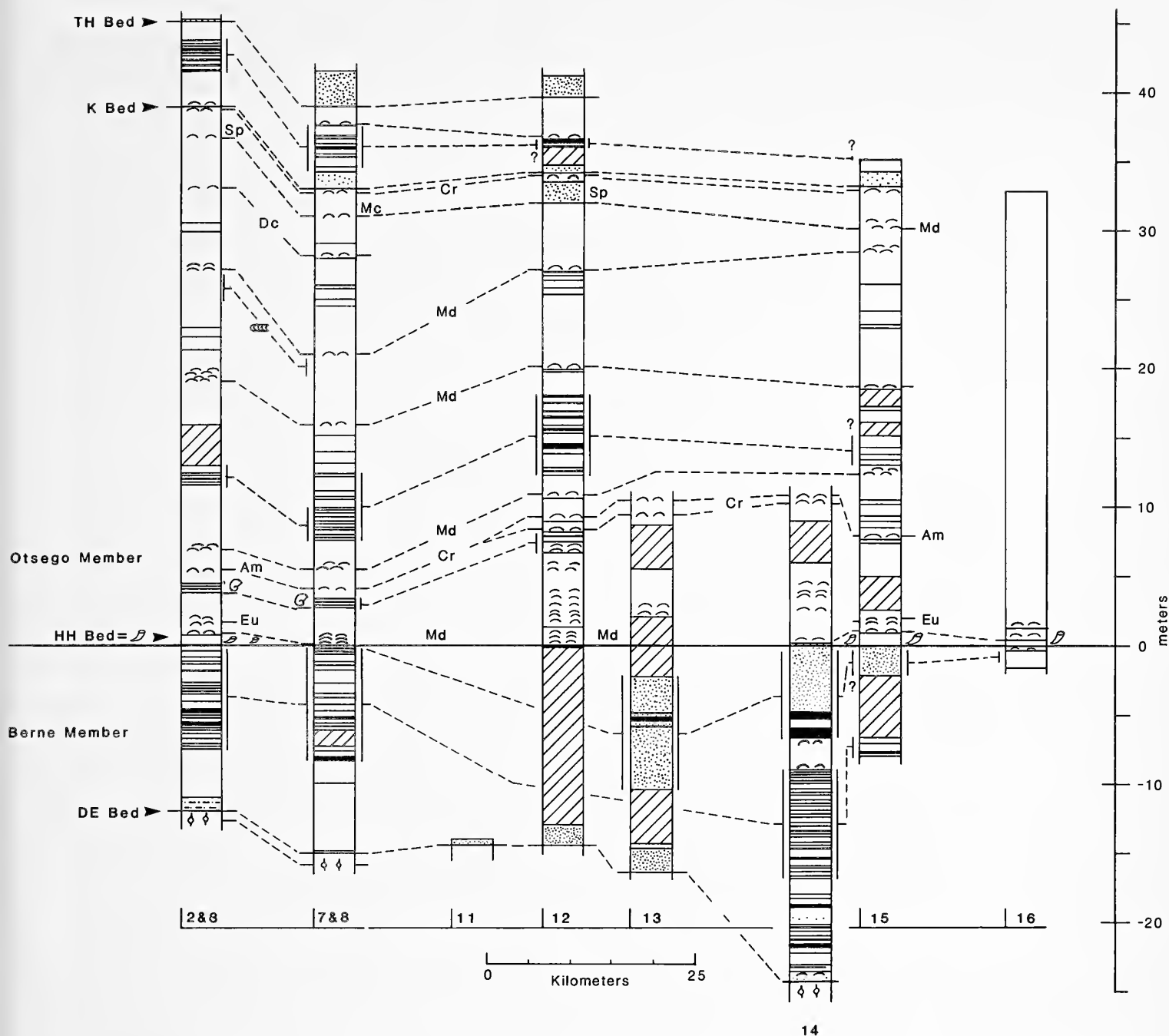


Figure 6. Regional correlations across the field area. For explanation, see key for Figure 5. Localities 2 to 14 lie along a line that is slightly oblique to the paleoshoreline. Localities 15 and 16 define a line that is perpendicular to the paleoshoreline.

sive sandstone is absent at Localities 9 and 10, and the shale unit with numerous shell beds overlies the intercalated thin sandstone and shale package of unit 1. Farther south, at Locality 8, the coral-brachiopod biostrome of the Halihan Hill Bed reappears and overlies unit 1 (see Figure 6). The massive sandstone unit reappears at Locality 1 and is overlain by the coral bed and the superjacent brachiopod-rich shale interval (see Figure 5).

The disappearance of the massive sandstone and the Halihan Hill Bed toward the more central localities along the outcrop belt is somewhat anomalous, because general lithologic and faunal trends throughout the study interval indicate these localities to be more proximal. The

generally coarser nature of sediments through the boundary of the members interval, and the occurrence of the diversely fossiliferous Halihan Hill Bed farther basinward than the other key beds (Loc. 15), appear to indicate deposition during a period of relative lowstand in sea level. Lithologic coarsening-up through units 1 and 2 during a relatively major drop in sea level was followed by deposition of the siliciclastic-poor, coral-rich Halihan Hill Bed (unit 3). Similar coral-rich units in the Hamilton Group have been interpreted by Brett and Baird (1990, p. A12) as deposits of the initial sediment-starved pulse of the ensuing transgression. The overlying shales with numerous shell beds of unit 4 mark continued transgression through the overlying interval.

Relative sea-level fall would cause increased incidence of normal and storm-wave erosive processes on the sea floor. This increased erosion may be responsible for the apparent local cut-out of the massive sandstone and the Halihan Hill Bed. Brett and Baird (1990, p. A12) recorded a similar occurrence of erosive beveling at the base of the Tichenor Limestone of the Hamilton Group in central and western New York State. Plint (1988) and Plint and Walker (1987) also discussed instances of erosive beveling associated with regressive maxima in the Upper Cretaceous Cardium and Bad Heart Formations of Alberta.

Erosive beveling and cut-out of the massive sandstone and Halihan Hill Bed may explain two seemingly anomalous features of the Berne–Otsego Member boundary interval. These features include lateral changes that involve lower faunal diversity, and lithologic fining in more proximal localities along the outcrop belt. These decreases in diversity and grain size contrast with the trends associated with the other three major key beds and other minor beds in the study interval. Erosive beveling of sections in the Hudson River Valley (Locs. 1–13) may also explain the anomalously thicker section (8–10 m thicker) between the Dave Elliott Bed and the base of the Otsego Member at Hannacrois Ravine (Loc. 14).

Origin of shell beds

Alternating shale–shell bed packages occur widely in the Hamilton Group (see Parsons et al., 1987) and have been noted in other epeiric sea and shallow-shelf settings (Fürsich, 1982; Bloos, 1982). A general model for genesis of packages of this type was proposed by Fürsich (1982). The model includes periods of a relatively high sedimentation rate that are represented by sparsely fossiliferous to barren shale intervals which did not allow colonization by sessile benthic organisms over a wide geographical range. However, Fürsich (1982, p. 218) stated that “extensive reworking by soft-bodied infaunal organisms was possible.” On the other hand, benthic faunas were able to establish themselves and flourish during relatively long periods of low-sediment accumulation. This resulted in the formation of widespread shell beds. Corrosion and boring of skeletal materials, along with the presence of authigenic phosphatic nodules and occasional fish debris in some shell beds, further indicate the genesis of shell beds during times of lowered sediment accumulation rate (Baird, 1978; Speyer and Brett, 1988).

Origin of thin sandstone packages

Relatively thin siltstone beds, similar to the thin siltstones to sandstones described above, were discussed by Brett et al. (1986b) from the upper part of the Hamilton Group of western and central New York State. Packages of these beds are part of coarsening-up sequences and feature planar laminations, cross-sets, or hummocky cross-stratification. The beds also display sharply defined basal surfaces, often with current lineations on their soles. Vertical escape burrows and vaguely developed graded bedding may be present. On the basis of the sedimentary structures, these thin siltstone beds were interpreted by Brett et al. (1986b) as tempestites that were deposited basinward after bottom-scouring during the peak of severe storms. This model for the formation of distal tempestites was outlined earlier by Aigner (1982).

Summary

Regional patterns in the shale-dominated upper part of the Berne Member and lower part of the Otsego Member of the Mount Marion Formation indicate that lithologic and faunal changes (summarized

below) are indicative of regionally widespread episodes of sedimentologic change in the eastern part of the northern Appalachian foreland basin at the time of deposition. A general shoaling-up trend through the entire study interval is punctuated by a relative lowstand in sea level at the boundary between the two members.

Dark grey to black argillaceous shales in the upper part of the Berne Member feature a fossiliferous, highly burrowed sandstone unit herein named the “Dave Elliott Bed.” Shales overlying the Dave Elliott Bed coarsen upward into a series of thin sandstone beds that have planar to hummocky cross-stratification. This interval of intercalated thin sandstones and shales is overlain to the north by a massive sandstone at the top of the Berne Member. The base of the overlying Otsego Member locally features a highly fossiliferous coral–brachiopod biostrome (Halihan Hill Bed), which is overlain by shales with numerous shell beds. The biostromal facies is apparently erosively cut out across the central 64 km of the outcrop belt, where the shell-bed-rich shales lie at the base of the Otsego Member. A general fining-up trend occurs through the 3.0 to 6.0 m-thick interval above the base of the Otsego; this is followed by a general coarsening-up trend to the top of the study interval. Relatively thick, argillaceous to silty shale intervals (ca. 1.0–8.0 m thick) punctuated by thin shell beds, with or without thin sandstone packages, characterize the lower part of the Otsego Member. Shell beds dominated by the brachiopod *Mediospirifer* characterize the approximately 24 m of section that overlie the Halihan Hill Bed. This is overlain by an interval with thin *Mucrospirifer*-dominated beds. Two massive, richly fossiliferous, *Zoophycos*-churned siltstone to sandstone units (Katsbaan and Timmerman Hill Beds) are found in the upper 7.0 to 9.0 m of the study interval; these two beds are separated by another package of thin sandstones and intervening shales.

Lateral lithologic trends include a relatively gradual coarsening of facies northward of Kingston. The coarsest facies apparently occur in the area north of Earlton near Locality 13. As the northerly part of the outcrop belt changes strike to NW–SE toward Clarksville, the lithologies generally tend to become finer. Westward from Clarksville the facies undergo a rapid change, and the section above the Halihan Hill Bed at Middleburgh is dominated by black shales. These patterns appear to indicate that the strand line was oriented roughly north–south, and that the basin center lay to the west.

Faunal patterns generally parallel these lithologic trends. Increasing diversity and a gradation toward faunas of more aerobic, shallower-water aspect characterize the various fossiliferous beds as they are traced northward from Kingston to Localities 12 and 13 on the Cocksackie 15-minute Quadrangle. A general decrease in diversity and a return to faunas of relatively more dysaerobic, deeper-water aspect occur in the shell beds along the outcrop belt from Locality 13 to East Berne (Loc. 15). The rapid change to black shales between East Berne and Middleburgh is accompanied by the disappearance of most of the marker units at Locality 16 in the Schoharie Valley.

Conclusions

Four key beds, packages of storm-generated siltstones to sandstones, and thin shell beds with characteristic faunas allow a microstratigraphic subdivision of a dominantly unfossiliferous shale interval in the Berne and Otsego Members of the Mount Marion Formation (Middle Devonian Hamilton Group) in eastern New York State. A nuculid bivalve–cephalopod association in the upper half of the Berne Member is succeeded by brachiopod-dominated associations of increasing diver-

sity and shallower-water aspect in the lower part (ca. 45 m) of the Otsego Member. Lateral faunal and lithologic variations across the outcrop belt indicate that shallower water conditions existed to the east, that the strand line was oriented close to north-south, and that the basin center lay to the west. Four formally named beds are proposed for the study interval in the Berne and Otsego Members: the Dave Elliott Bed, Halihan Hill Bed, Katsbaan Bed, and Timmerman Hill Bed. A revised definition for the base of the Otsego Member places it at the base of a coral-brachiopod biostrome, the lowest rugose coral in a massive sandstone, or the top of the massive sandstone (in the absence of corals in the sandstone). In the absence of both the coral biostrome and the massive sandstone, the base of the Otsego Member is placed at the lowest shell-bed-rich shales that overlie an 8.0 m-thick package of thin sandstones and shales. Regional lithologic and sedimentologic analysis indicates that the base of the Otsego Member is somewhat diachronous, apparently due to local erosive beveling of a massive sandstone and the Halihan Hill Bed during a relative lowstand of sea level.

Acknowledgments

The author wishes to express gratitude to E. Landing for guidance and encouragement from the inception of this project. Additional appreciation is expressed to C.E. Brett for discussions in and out of the field. C.E. Brett and B.W. Selleck provided critical reviews of this paper. The author also thanks C. Gregory for assistance in preparation of the manuscript. This research was part of a program of study that led to a Bachelor of Science degree from Empire State College (State University of New York). Fieldwork was funded, in part, by the New York State Geological Survey. Faunal and lithologic specimens that were the basis of faunal/stratigraphic/sedimentologic interpretations are deposited in the New York State Museum Paleontology Collection under locality numbers 9366-9490.

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**ISSN-0278-3355
ISBN-1-55557-196-4**